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Structure and dynamics in mixed forest stands of interior Alaska

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STRUCTURE AND DYNAMICS IN MIXED FOREST STANDS OF INTERIOR ALASKA

A

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STRUCTURE AND DYNAMICS IN MIXED FOREST STANDS

OF INTERIOR ALASKA

By

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ABSTRACT

This study examines aspects of stand development in young mixed hardwood-conifer forests on upland sites in interior Alaska, with the goal of refining concepts of plant community succession. Specific objectives were: *i*) describe the structural characteristics of young mixed hardwood-conifer stands, including composition, horizontal and vertical arrangement and component size; *ii*) define common stand development patterns; *iii*) compare juvenile height and diameter growth increments for the different species; *iv*) correlate existing stand structure with stand-disturbing events; and *v*) suggest considerations for manipulating stand structure and composition of mixed stands to maintain productivity and provide a variety of forest products. Techniques involve the study of disturbance events, establishment and growth patterns following disturbance and the resulting stand structure. Procedures used were: *i*) develop a community type classification to partition the variability within the ecosystem into units having similar floristic features; *ii*) determine the successional trends within each community type by reconstructing the growth patterns along a chronosequence; *iii*) describe common structural attributes of the community types and relate these to stand dynamics; and *iv*) develop height growth relationships and estimates of productivity by species within the

community types.

A total of 53 upland mixed communities were sampled and classified into five community types: **Populus tremuloides/Arctostaphylos uva-ursi**, **Populus tremuloides/Shepherdia canadensis**, **Betula papyrifera-Populus tremuloides/Viburnum edule**, **Betula papyrifera-Populus tremuloides/Alnus crispa** and **Picea glauca-Betula papyrifera/Hylocomium splendens**. Community types were described on the basis of distribution and physical environment, vegetation composition and structural features, successional relationships of stand development, productivity estimates and relationship to previously described vegetation units. Two stand development patterns were identified. The first pattern was rapid establishment of hardwoods, followed by prolonged establishment of conifers. This pattern describes development within the **Populus tremuloides/Arctostaphylos uva-ursi** and **Populus tremuloides/Shepherdia canadensis** community types. In contrast, a second pattern occurring most often in the remaining three community types was one of rapid concurrent establishment of hardwoods and conifers. Productivity of open-grown conifers was differentiated from that of stand-grown or suppressed conifers. Estimates of productivity are generally dissimilar to those for pure, even-aged and fully stocked stands.

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INTRODUCTION

Stands containing mixtures of conifers and hardwoods are not often encouraged in intensive forest management in North America (Oliver 1980). Management is often complicated by possible differences in growth rates, the non-uniform stem sizes and qualities and thus higher costs of harvesting, and also the unreliability of volume tables and growth and yield predictions. Traditionally, forest management in western and northern North America has emphasized the creation and culture of stands consisting of a single species of conifer. Yet the boreal forest of interior Alaska consists of various mixtures of conifers and hardwoods. Existing characterizations of forest stand structure and projections of growth (Gregory and Haack 1965, Farr 1967) do not adequately represent conditions within the upland mixed forest within interior Alaska because they are based on pure, even-aged, fully stocked stands.

Understanding the basis for changes that occur in the sequential development of forest stand structure, or forest dynamics, is fundamental to forest management. This study examines several aspects of stand development in young mixed conifer-hardwood forests on upland sites. Techniques involve the study of growth patterns within young stands, disturbance patterns and the stand structure resulting from such disturbances.

Previous work

Functional relationships of interior Alaska forest ecosystems, emphasizing the controlling role of soil temperature and forest-floor chemistry in secondary succession and their affect on biomass productivity and nutrient cycling, have been studied for several decades (Van Cleve and Viereck 1981, Van Cleve *et al.* 1983, Flanagan and Van Cleve 1983). The effect of recurring fire as a dominant disturbance event in most forest communities is also well documented (Lutz 1956, Slaughter *et al.* 1971, Dyrness *et al.* 1986), although the role of fire within the *Picea mariana*[1] ecosystem has received the most attention.

A general hypothesized model (hereafter referred to as the Van Cleve and Viereck model) was developed for predicting autogenic successional relationships of upland conifer-hardwood forests under natural conditions (Viereck 1975, Van Cleve and Viereck 1981, Yarie 1981). The time gradient represented by this model is partitioned into discrete vegetation types for different successional stages (Van Cleve and Viereck 1981, Foote 1983, Yarie 1983). The model suggests that succession is orderly, directional and predictable (McIntosh 1981) and culminates with the dominance of *Picea glauca*. This scenario suggests that *P. glauca* seed is available, and germination and establishment of *P. glauca* is concurrent with hardwood regeneration. Development of mixed stands from concurrent establishment of

[1] Taxonomic nomenclature for plant species observed in this study is presented as appendix A.

conifers and hardwoods, however, has not been demonstrated adequately for various sites in interior Alaska.

The Van Cleve and Viereck model of forest succession is relatively restrictive. It fails to encompass possible successional relationships resulting from disturbance events other than stand-replacing fires. It also falls to incorporate possible successional stages for which propagule availability is limited or restricted. Successional sequences following other types of disturbances need to be described.

Insects, disease, wind, or mechanical disturbances (timber harvesting) create gaps in the overstory canopy and growing space on the forest floor, and may lead to the recruitment of new stems. Species composition of regeneration may differ from that predicted by the Van Cleve and Viereck model of succession as a result of the size of gap created through disturbance. Propagules may be limited because of distance from an adequate seed source or inadequacies of the seedbed. Regeneration within gaps also will create stands with multiple age-classes, especially if the gaps are slow to fill because of poor *P. glauca* seed distribution.

Timber inventory data for interior Alaska (Hegg 1975) indicate that upland stands contain fewer conifer stems than suggested by the Van Cleve and Viereck model of succession. Interior Alaska *P. glauca* seed production is irregular and periodic, and is strongly influenced by several environmental

factors (Zasada 1980, Alden 1985). A disparity in *P. glauca* regeneration may have occurred over the last sixty years because of wide-spread removal of cone-bearing trees through high-grading--partial-cutting of the larger diameter stems for fuelwood and mining timbers (Lutz 1963, Zasada *et al.* 1977, Herman 1978).

Current management practices which emphasize clearcutting without regard for adjacent seed sources may also encourage departures from the Van Cleve and Viereck successional model because natural regeneration of hardwoods is rarely controlled. This presents several questions for consideration: *i*) will hardwood stands that contain little or no conifer regeneration following the stand-initiating disturbance ever develop into pure, even-aged, fully-stocked *P. glauca* stands; and *ii*) will past high-grading and present-day selective cutting of *P. glauca* result in regeneration of hardwood species, release of advance regeneration of *P. glauca*, or germination and establishment of *P. glauca* seedlings?

Use of Stand Development Studies

Stand development studies involve identification and description of changes in forest stand structure over time. From the interactions within a stand come the finite set of silvicultural treatments to produce desirable stand growth patterns meeting specific objectives. Numerous stand development studies have helped

focus forest management objectives by predicting future stand structure and development patterns, reducing silvicultural costs, increasing stand productivity and obtaining desired species mixtures (Oliver and Larson 1990).

The study of forest stand development has long been an integral component of forest succession studies, yet only recently has it been distinguished as a rather narrow discipline within the general studies of forest ecology and silviculture (Oliver 1982). Perhaps the first work was that of Stephens (1956) who investigated growth rings and stem positions as a method of determining historical trends in forest stand development. In their second edition of the classic forest ecology text, Spurr and Barnes (1973) recognized the role of disturbance in altering the structure of forest stands. More recent work has emphasized the forest disturbance history of various stands, especially the creation of openings within overstory canopies and the subsequent invasion or regeneration within gaps (Hemstrom 1979, Runkle 1981, Hibbs 1982, Jaeck *et al.* 1984, Glitzenstein *et al.* 1986). This type of work usually involves labor-intensive procedures (Lorimer 1985) and thus is not normally applied on a regional basis.

Oliver (1982) distinguished analysis of chronosequences, re-examination of permanent plots, consideration of species autecology, comparison of stand physiognomy and reconstruction of growth patterns as methodologies in forest stand development studies. A chronosequence is a series of stands of different

age, all of which have the potential for developing similar structure at some point in time. Stands within a chronosequence should develop on similar sites with similar soils and climate, have similar disturbance histories and have similar species composition. A principal problem with this technique is the identification of stands having different ages but occurring on sites having similar environmental conditions. Periodic re-examination of permanent plots has the advantage of providing undisputable evidence of change within a true chronosequence, yet few workers have the time or funding to establish plots and wait the length of time necessary to document structural changes. Making inferences of stand development patterns from species autecological characteristics involves determining the environmental conditions in which a given tree species would have a competitive edge based on physiological characteristics such as seed dispersal, photosynthetic efficiency, root development or allelopathy (Harper 1977). Making inferences about stand development patterns from stand physiognomy involves describing the distribution of trees by age or size class, horizontal or vertical spatial patterns of stand components, or the distribution of stand biomass into different strata. Reconstruction of past growth patterns involves detailed aging of stems or examination of dead stems, bark or root collars to determine height growth patterns, changes in species composition or times and types of past disturbances.

From a practical sense, one method or technique alone is rarely sufficient, and a combination of techniques is necessary if sound inferences are to be drawn.

The length of a chronosequence is limited by the most recent stand-replacing event. In eastern North America, the most common form of chronosequence study is the "old field succession" in which sites of assumed similar ecological potential differ in the length of time since abandonment from farming or similar activity. Throughout western North America, fire plays a dominant role in stand replacement, and dictates the potential length of chronosequences. Forest dynamics along mesic canyon bottoms in a portion of the Bitterroot Mountains of Montana where shown to be driven by initial floristic composition of both shade-tolerant and shade-intolerant tree species based on a chronosequence of 32 stands, with time since last replacement varying from 70 to 240 years (McCune and Allen 1985). Examination of over 200 western Washington stands within two habitat types, arranged along a fire-free chronosequence approximately 700 years long, indicated differences in height growth of dominant *Pseudotsuga menziesii* (Mirb.) Franco between habitat types and a deviation from the height growth patterns presented for published site index curves (Henderson 1982). Cogbill (1985) used a combination of reconstruction of growth patterns from tree cores and a chronosequence of sites within four general vegetation categories to disprove the hypothesis of continual

recruitment leading to an all-aged forest in central Quebéc. Similar techniques were used to describe patterns of forest development on recently deglaciated sites on which different disturbance events resulted in different species compositions, although stands had similar physiognomies (Oliver *et al.* 1985).

Inferences of stand development patterns from stand physiognomy--the stem architecture, method of stem origin, sizes of component stems, or distribution of trees by age or size class, have been made by a number of workers. Hanley *et al.* (1975) used differences in age classes to describe uneven-aged stands of *Picea engelmannii* Parry, *Abies lasiocarpa* (Hook.) Nutt. and *Populus tremuloides* and to recommend the use of uneven-aged (selection) silvicultural systems in the management of these high elevation stands of southern Utah. Kelty (1989) documented greater yields and higher rates of total basal area accumulation in mixed stands of *Quercus rubra* L. and *Acer rubrum* L. with *Tsuga canadensis* (L.) Carr. compared to stands containing *Q. rubra* and *A. rubrum* without *T. canadensis*. Steijlen and Zackrisson (1987) attributed variation in the age structure and invasion pattern of small gaps in a single mixed stand of *Pinus sylvestris* L., *Picea abies* (L.) Karst. and *Betula pubescens* Ehrh. in northern Sweden to climatic fluctuations influencing seed production, germination and early survival of seedlings. Diameter-class distribution, stand age and community composition were used to distinguish between two community types in *Fraxinus latifolia* Benth. forests in central

Oregon and their development following the cessation of burning and grazing (Frenkel and Heinitz 1987). Juday and Zasada (1984) used size- and age-class distributions and height profiles to describe mature *P. glauca* stands on floodplain sites in interior Alaska, and to hypothesize successional trends of stand development.

Procedures for reconstruction of growth patterns are described by Duff and Nolan (1953) and Henry and Swan (1974). Reconstruction of *P. menziesii* diameter-growth patterns in two adjacent stands on opposing aspects revealed different stand dynamics, yet both stands had similar uneven-aged structures (Tesch 1981). Stem analysis and reconstruction of height-growth patterns in three young *Tsuga heterophylla* (Raf.) Sarg. stands revealed similar patterns of canopy differentiation, dominant height growth and dominance assertion after previous disturbance, in spite of marked differences in appearance (Jaeck *et al.* 1984).

Reconstruction of growth pattern is a principal analytical technique for comparing growth of component species in mixed stands. Veblen *et al.* (1989) used dendrochronological analyses for reconstruction to investigate stand development in relation to large-scale blowdown and insect-caused mortality in subalpine forest of *Pinus contorta* Dougl., *Abies lasiocarpa* and *Picea engelmannii* in the Colorado Front Range. These workers suggested the need for incorporating various disturbance events into explanations of stand

development in similar forests. Reconstruction has improved predictions of yield by species in mixed stands of *P. menziesii* and *Abies grandis* (Larson 1986), and *Abies amabilis* Dougl. ex Forbes and *Tsuga heterophylla* (Murray and Leonard 1990). Reconstruction with emphasis on growth of advance regeneration and competitive interactions following disturbance in mixed stands has contributed to an understanding of species diversity and implications for intermediate cutting within various ecosystems, including mixed hardwood-pine forests of east Texas (Glitzenstein *et al.* 1986), mixed temperate floodplain hardwood forests of Arkansas (Oliver *et al.* 1990), mixed northern hardwood forests of Wisconsin (Hix and Lorimer 1991) and mixed coastal coniferous forests (Harcombe 1986, Deal *et al.* 1991).

Objectives

The underlying goal of this study of forest stand development was refining concepts of plant community succession on upland sites in interior Alaska. Specific objectives were: *i*) describe the structural characteristics of young mixed hardwood-conifer stands, including composition, horizontal and vertical arrangement and component size; *ii*) define common stand development patterns; *iii*) compare juvenile height and diameter growth increments for the different species; *iv*) correlate existing stand structure with stand-disturbing events; and *v*) suggest various considerations for manipulating stand structure

and composition of mixed stands to maintain productivity and provide a variety of forest products.

From a practical view, the results are most applicable in improving silvicuitural prescriptions and forest management plans. Documenting the potential for managing *P. glauca* and its associated hardwood species under either even or uneven-age systems should assist forest resource managers. By understanding the growth patterns of the different species and species mixtures, estimates of stand production will be improved.

Hypotheses

Two working hypotheses were developed to provide guidelines for this study of stand dynamics and tests of new field procedures. The first hypothesis is that conversion of a stand of hardwoods to conifers occurs through a gradual invasion of conifers in an even-aged hardwood stand. This process fits the "tolerance" model of Connell and Slatyer (1977) and has been suggested as appropriate for a single site near Fairbanks, Alaska (Quirk and Sykes 1971). Evidence in support of this hypothesis would be significant differences within the age-ciass distribution of *P. glauca* and between *P. glauca* and hardwoods for stands across different sites. Evidence for rejection would require a pattern of single-age classes (or several closely spaced age-classes) for stands on different sites. Rejection of this hypothesis would then support the concept of

different forest communities having equal potential for indefinite dominance (Oliver 1981, Glenn-Lewin 1980), or, that succession proceeds along different pathways for similar sites.

The second hypothesis is that productivity of *P. glauca* growing with hardwoods in mixed stands is equal to that of *P. glauca* in pure stands on similar sites. Evidence in support of this hypothesis would be estimates of productivity for *P. glauca* in mixed stands similar to mean breast-height age, site index and volume relationships as reported by Farr (1967) for pure *P. glauca*. Evidence for rejection would be differences in mean breast-height age, volume and site index relationships between pure stands as reported by Farr (1967) and mixed stands.

THE ENVIRONMENTAL SETTING

Physiography, geology and soils

Interior Alaska is broadly defined as the area bounded by the Alaska Range to the south, the Brooks Range to the north, Nulato Hills and Seward Peninsula to the west, and the US-Canadian border to the east, with the city of Fairbanks roughly in the center. Within this vast area, forests extend from near sea level to over 900 m in elevation. Cutting through this area are numerous major rivers with broad floodplains, including the Yukon, Tanana, Kuskokwim, Chatanika, Kantishna and Tolovana rivers. Floodplain ecosystems were excluded from this study because of major differences in disturbance regimes, site factors and species compositions.

The Yukon-Tanana uplands lie between the Yukon and Tanana rivers and consist of approximately 78 thousand square kilometers of mostly unglaciated rounded hills and ridges (Schoephorster 1973). Only on a few isolated peaks have Pleistocene alpine glaciers steepened the valley walls. The northwest portion of the Yukon-Tanana uplands, bounded by the Tanana River, the Tintina fault zone, and the Shaw Creek Fault, is defined as the Fairbanks-Big Delta region (Schoephorster 1973). Bedrock of this region is primarily metamorphic rocks, including quartz-mica schist, greenschist and quartz-mica gneiss (Foster *et al.* 1973). This region differs structurally and stratigraphically from the

eastern region of the Yukon-Tanana uplands, which contains concentrations of igneous rocks. The area of consideration in this study is the upland portion of the Fairbanks-Big Delta region drained by the Tanana River and its main tributaries of Shaw and Goldstream creeks and the Salcha, Chena, Chatanika, Tatalina and Tolovana rivers (Fig. 1). Elevations within the study area range from nearly 110 m on the Tanana River at Nenana to over 1600 m at Mt. Prindle in the White Mountains north of the Chatanika River.

Except for a few eroded areas, uplands within the study area are covered by a mantle of silty micaceous loess derived from outwash plains on the northern flanks of the Alaska Range. Loess deposits range from a few centimeters at upper elevations near the Yukon River to over 50 m on toeslopes near the Tanana River. Most soils developing in this loess have silt loam textures.

Permafrost is a common feature of many landscapes at this latitude, but is discontinuous in the uplands. North-facing slopes, alluvial terraces, flat benches and depressions filled with organic matter may have ice near the soil surface. South-facing slopes generally lack permafrost, are relatively warm and dry, and are subject to negligible leaching because of high evapotranspiration (Van Cleve *et al.* 1991). The majority of soils on south-facing slopes are classified as Inceptisols which indicate moderate development with weakly expressed horizons. All have formed under either a cryic or pergelic temperature regime; some have formed under an aquic moisture regime.

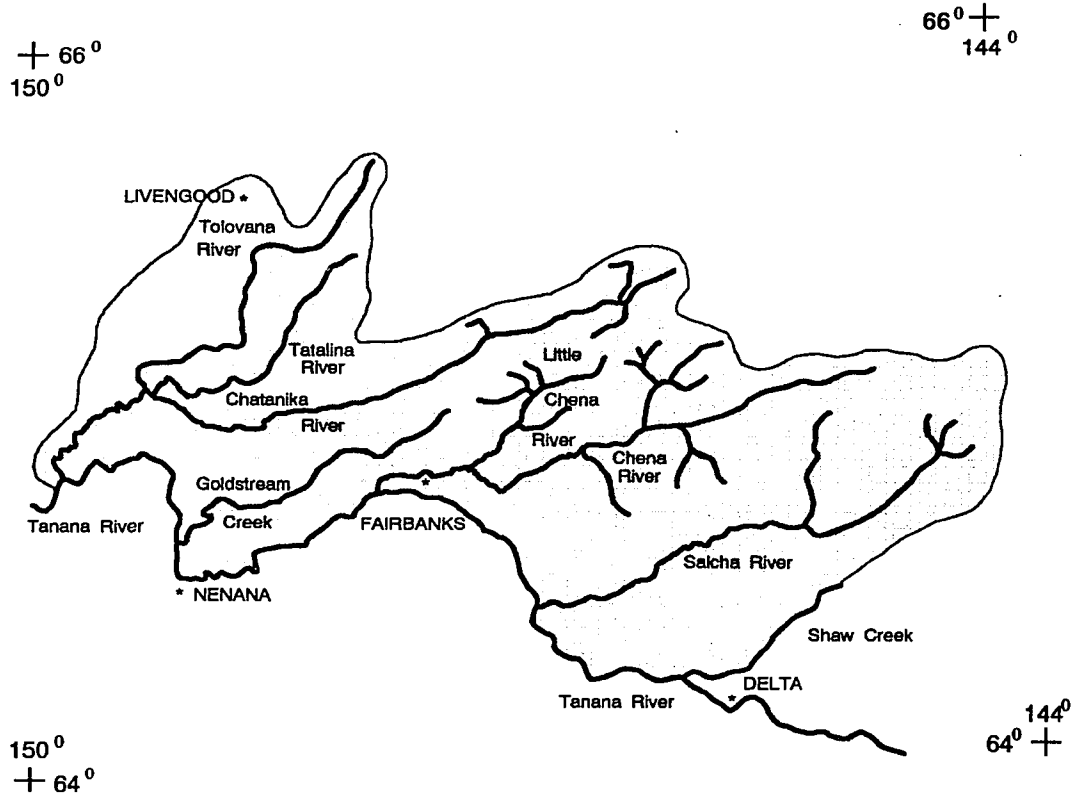

FIG. 1. Area covered by this study (shaded) showing major drainage patterns and towns. Scale: 1 cm = 16 km.

Climate

Climate of the study area is continental and is characterized by extreme annual and diurnal temperatures, low precipitation and little wind. Near Fairbanks, the mean temperature in January is -25° C and the mean temperature in late June is 18° C (Bowling 1984). Total seasonal range is more than 80° C. Strong wintertime inversions are common, with minimum temperatures moderated as much as 10° C with an increase of 150 m in elevation. Temperature differences at various locations within the study area are often extreme because of aspect and elevation.

Total annual precipitation near Fairbanks averages 285 mm; 35 percent falls as snow. Snow cover persists from October through late April. The growing season averages 97 frost-free days (Slaughter and Viereck 1986). Mean maximum snow depth of nearly 60 cm occurs by February. Snowpacks in forested areas are characterized by low density at initial deposition and extensive development of depth hoar (Slaughter and Viereck 1986). Snowpack ablation begins on southern aspects with increasing day length in March.

Summer precipitation across the study area is more variable than winter snowfall; differences are attributed to orographic effects and local environments (Haugen *et al.* 1982). Most of the summer precipitation falls during late July and August as a result of low pressure centers located near the Bering Strait (Bowling 1980, Bowling 1984).

Extreme seasonal variation in day length and sun angle are characteristic of

the high-latitude location of the study area and contribute greatly to the extreme variation in available solar radiation. At latitude 65°N, the sun is above the horizon for 18 to 21 hours daily during the summer months of May through July; conversely, only 3 to 6 hours of potential sunlight occur during the winter months of November through January. The solar angle varies from 2.5° at the winter solstice to 48.5° at the summer solstice (Slaughter and Viereck 1986), resulting in direct short-wave radiation received obliquely on horizontal surfaces.

The remoteness of the study area is reflected in the presence of only three National Weather Service recording stations: Nenana Municipal Airport, Fairbanks International Airport and Eielson Air Force Base; all are located along the Tanana River at low elevations. Appendix B presents a comparison of long-term averages from two of these stations with data from a recently installed weather station on a mid-slope site in Bonanza Creek Experimental Forest west of Fairbanks, which may better reflect conditions on upland forested sites.

Floristics and silvics

Forests of interior Alaska are sometimes referred to by the term *taiga* because of similarity to open coniferous forests of eastern Asia (Viereck 1975). These forests are also an extension of the boreal forest zone spanning much of Canada (Larsen 1980). At the landscape level, upland forests are a mosaic of small stands with various mixtures of conifer and hardwood species. This

upland conifer-hardwood forest complex covers about 261 thousand square kilometers between the Alaska and Brooks ranges (Neiland and Viereck 1977), of which about 91 thousand square kilometers is considered commercial forest (Zasada and Argyle 1983). More than 65 percent of the total land base within the Tanana Valley State Forest consists of mixed stands of conifers and hardwoods (Alaska Department of Natural Resources 1986). The complex consists of overstories of *Betula papyrifera*, *Populus tremuloides* and *Picea glauca* and lesser amounts of *Populus balsamifera* and *Picea mariana*. Beneath the conifer and hardwood overstory, undergrowth layers are dominated by shrubs, including *Alnus crispa*, *Rosa acicularis*, *Viburnum edule* and *Vaccinium* species. Zackrisson (1985) reviewed distribution patterns and evolutionary aspects of life history characteristics for these boreal forest species, especially their adaptations for survival during Pleistocene climatic changes, and their adaptations for survival following fire.

A comprehensive state-wide vegetation classification system designed to categorize existing vegetation, under development since 1976, incorporates four levels of resolution (Viereck *et al.*, in prep.). Mixed stands of hardwoods and conifers sampled in this study may belong to one of the following categories: Closed Paper Birch Forest (I.B.1.d.), Closed Quaking Aspen Forest (I.B.1.e.), Closed Paper Birch-Quaking Aspen Forest (I.B.1.f.), Open Quaking Aspen Forest (I.B.2.b.), Open Paper Birch Forest (I.B.2.a.), Closed Quaking Aspen-

Spruce Forest (I.C.1.d), or Closed Spruce-Paper Birch-Quaking Aspen Forest (i.C.1.f.).

A common feature of closed canopy, conifer-dominated stands in these high-latitude forests is development of a thick moss mat on the forest floor, primarily of the feathermosses *Hylocomium splendens, Pleurozium schreberi* and *Rhytidiadelphus triquetrus.* Species diversity of forbs, graminoids and shrubs is low compared to more southern forests. Many species such as *Deschampsia caespitosa, Linnaea borealis, Potentilla fruticosa, Epilobium angustifolium, Empetrum nigrum, Ledum palustre, Arctostaphylos uva-ursi, Juniperus communis* and *Vaccinium vitis-idaea* have circumboreal distributions. Extensions of Rocky Mountain floras often occupy the warmest and driest microsites, and include *Agropyron spicatum, Amelanchier alnifolia, Apocynum androsaemifolium, Shepherdia canadensis* and *Zygadenus elegans.*

P. glauca cone and seed production is irregular and enhanced by warm, dry summers (Zasada 1980). Factors leading to low production of seed include unusually cool temperatures during cone initiation, nutrient deficiencies, insects, disease and squirrels (Alden 1985, Nienstaedt and Teich 1972, Zasada 1980, Zasada *et al.* 1978). Dispersal begins in late August, peaks in September and October, and gradually tapers to sporadic seedfall through the following April and May (Zasada 1985, Zasada and Viereck 1970). Wind is the primary agent for dispersal of seed. Negative exponential models predicting dispersal of filled

seed into openings indicate that seed for natural regeneration on mineral seedbeds may be adequate up to 120 m from the opening edge in years of relatively high seed production (Youngblood and Max 1992).

Within the study area, germination of *P. glauca* occurs from mid-May to late July, beginning with the warming of seedbed surfaces. Exposed mineral soil provides the best seedbed, however, some germination occurs on decayed logs and stumps. Establishment on layers of *Hylocomium splendens* and other feathermosses is infrequent, apparently in response to moisture limitations. Early growth is slow, with root development exceeding shoot development. Experiments with a simulation model indicated the probability of obtaining adequate *P. glauca* restocking with natural regeneration after timber harvest was poor, and was sensitive to assumptions of initial seedbed condition, frequency of good to excellent seed years and the rate of establishment for competing vegetation (Fox *et al.* 1984).

Seed is produced by mature *B. papyrifera* trees almost every year, although production varies between trees, stands and years. Dispersal begins soon after ripening in August through early September and remains high through November; some seed may continue to fall for several months depending on weather conditions (Zasada 1985). The light, winged seeds are dispersed readily by wind, with sufficient seed for regeneration of 30-m wide openings occurring in at least one of every four years (Zasada and Gregory 1972).

Establishment and early growth is best on mineral soil surfaces in response to greater moisture and nutrient availability (Zasada and Grigal 1978)

P. tremuloides is a dioecious species. Seed is produced on female trees in most years in May. Dispersal of seed is by wind, and occurs shortly after seeds ripen through June. Germination is rapid over a wide range of temperatures, although high and continuous availability of water is critical, and viability is lost after several weeks (McDonough 1979). Initial shoot growth is more rapid than root development, and moisture and nutrient absorption occurs through fine root crown hairs (McDonough 1985). Establishment is best on well-drained but moist mineral seedbeds. Failures occur due to unfavorably high surface temperatures, rapid drying of the soil surface or presence of inhibitors in the soil or litter (McDonough 1985).

Most upland stands of *P. tremuloides* within the study area are the result of root sucker development. Adventitious shoots on lateral roots occur first as meristems in the cork cambium that develop into buds and then shoots, but are held dormant by apical dominance (Schier 1973). Following disruption of apical dominance by burning, cutting or defoliation, adventitious shoots along the lateral roots erupt and develop into rametes. Genetically identical suckers have interconnected root systems, and the resulting stand is a clone.

Disturbance history

Wildfire is a common disturbance event in much of the upland forests of interior Alaska (Viereck 1975). The natural fire regime of mature *P. glauca*-dominated stands within the region has been characterized by fire type and intensity, size and frequency or return interval (Lutz 1956, Barney 1971, Viereck and Schandelmeier 1980, Heinselman 1981). These stand-replacing disturbances are either high-intensity crown fires or severe surface fires. Almost 25 thousand square kilometers burned during 19 individual fires in the early settlement and mining period of 1893 to 1937. During the period 1950 to 1969, there were almost 1,600 lightning-caused fires in the interior which burned an average of 30 square kilometers, in addition to over 4,900 man-caused fires which burned an average of 14 square kilometers. Year-to-year variability is high, however, with years of greater than normal numbers and size of fires occurring sporadically. Extreme fire seasons occurred in 1940, 1957, 1969, 1977 and 1988. Fire cycles, the time required to burn an area equivalent to the area in question, are between 150 and 250 years.

Within the study area, wildfires in *P. glauca* stands occur most frequently during June and early July and are associated with early summer temperature and moisture patterns. Surface fires are carried by litter and the upper layers of dried moss, and are easily transformed into crown fires with abundant ladder fuels created by lower branches. *P. glauca* has relatively thin bark and shallow

roots and is easily killed by even light surface fires.

In contrast, fire regimes for hardwood ecosystems are largely unknown. Stands dominated by *P. tremuloides* or *B. papyrifera* are most susceptible to fire immediately following snow melt and prior to leaf bud burst, when leaf litter on the forest floor may carry light surface fires. At this time, snow patches may still remain in surrounding conifer-dominated stands. These hardwood species are thin-barked and can be killed by surface fires. Following shrub and tree leaf development, high live fuel moisture may prevent the spread of fire, which often stops at these community boundaries. Yarie (1981) suggested a fire cycle of 26 years in hardwood stands in the Porcupine drainage of northeastern Alaska, an area which receives less precipitation than the area studied here.

Foote (1983) outlined a general progression of successional stages following a replacement fire on warm upland sites. The initial stage, lasting through the first five years, is characterized by establishment of light-seeded species such as *Epilobium angustifolium* and *Salix scouleriana* and ground mosses. Species such as *P. tremuloides*, *Viburnum edule, Rosa acicularis* and *Geranium bicknellii* that regenerate from buried root systems or buried seed also occur. The next stage after fire is the development of tall shrubs and saplings. Following this is a 25-year period characterized by dense stands of woody stems. Beginning 50 years after fire and lasting for about 100 years is a hardwood stage during which species competition leads to gradual reduction in

stem density and a dominance of *P. tremuloides* or *B. papyrifera* in a mature canopy. After 150 years, *P. glauca* replaces hardwoods in the overstory canopy.

Several species of insects are known agents of disturbance in upland hardwood forests of interior Alaska (Werner 1977, Werner 1979, Werner 1986). The large aspen tortrix, *Choristoneura conflictana* Walker, is a serious pest of *P. tremuloides* throughout northern forests of North America and periodic outbreaks within the study area are common. Repeated defoliation for a 2-year period may cause reduced radial and terminal growth; additional defoliation may result in tree mortality. Defoliation increases light availability for undergrowth species and may lead to suckering in *P. tremuloides* root systems because of disruption of overstory apical dominance. *P. tremuloides* stands are often completely defoliated for two consecutive years, then recover as insect populations subside. The spear-marked black moth, *Rheumaptera hastata* L., attacks primarily *B. papyrifera*. Epidemic populations occur at 15- to 17-year intervals, persist for two years and then collapse. Host radial and terminal growth is reduced, spring bud development is delayed and branch dieback is common. More light may be available in the undergrowth for shrub and seedling growth because of tree canopy defoliation.

Human disturbances in upland forest communities began at least 12,000 years age with the Gwich'in and Tanana cultures, aboriginal Native Americans

who used the forest resources of wood, fuel and berries. Nomadic families living in remote camps cut *P. glauca* to construct food caches, shelters and miles of fences to concentrate migrating caribou herds (Helm 1981). Gold was discovered in the Yukon Territory in 1896 and in interior Alaska in 1902, leading to a wave of miners and settlers. Much of the subsequent stand disturbance was cutting of fuelwood for settlements and stern-wheel paddle boats, and logs for mine props and construction material. In addition, vast areas were intentionally burned to melt frozen soils, with many fires allowed to escape and consume forested hillsides away from patented lands. From 1910 through 1920, an estimated 60,000 cords of firewood were cut and utilized annually in Fairbanks and nearby mining camps (Sampson *et al.* 1983).

METHODOLOGY

This study of stand development in interior Alaska seeks a concurrence of inferences from different techniques, including examination of chronosequences, stand physiognomy and reconstruction of growth patterns. Procedures were: *i*) develop a community type classification to partition the variability within the ecosystem into recognizable and discrete units having similar floristic features; *ii*) determine the successionai trends within each community type by reconstructing the growth patterns of existing stands along a chronosequence; *iii*) describe common structural attributes of the community types and relate these to successional trends and chronosequences; and *iv*) develop height growth relationships and estimates of productivity by species within the different community types.

Field Methods

The objective of field sampling was to collect data across the full range of environmental conditions supporting young mixed stands throughout the Fairbanks-Big Delta region uplands. Data for this study came from sites north of the Tanana River from Delta to Nenana, and as far north as Livengood (Fig. 1). Field work occurred during the summers of 1987 to 1990.

Site Selection -- Reconnaissance of forest sites was made prior to site selection. False-color aerial photography was available for some portions of the study area and was used to locate potential sites. The normal procedure was to travel an elevational transect along a river, road or trail system keeping a mileage log of changes in plant community patterns. Brief stops along transects permitted inspection of both overstory and ground cover composition. At the end of the transect the log was inspected and representative sites selected for sampling. Sites were selected with a "subjective but without preconceived bias" approach (Mueller-Dombois and Ellenberg 1974) in that sites met certain requirements. Sites were not selected, however, with any preconception of placement within a classification. Criteria for site selection were: *i*) vegetation homogeneous and representative of other sites within the landscape; *ii*) tree strata composed of *Picea glauca* and at least one deciduous hardwood species; *iii*) apparent age of the dominant stems in the stand between 25 and 100 years of age at the ground; and *iv*) lack of dominance of *Picea mariana*. Exclusion of sites supporting extensive coverage of *P. mariana* was necessary to restrict the study to the warmest sites with highest productivity.

Site Description -- Each temporary sample plot was circular and slope corrected to be 375 m^2 in size. Plot center was subjectively located within the stand to sample a representative portion of the dominant plant community

composition and to avoid obvious ecotones that might occur at stand edges, recently disturbed canopy gaps, or unusual microsites. Photos were taken of each community showing both the undergrowth and overstory composition.

Notes were made on the physical factors of each site, including slope, aspect and relative slope position and configuration. Elevation was estimated to the nearest contour using U.S. Geological Survey 15-minute quadrangle maps. Evidence of recent perturbations and potential successional relations were noted, including location of *P. glauca* seed sources, juxtaposition, insect and disease occurrence and presence of charcoal in the forest floor or charred snags.

Ocular estimates of canopy cover for all vascular species within the plot were made to the nearest percent between 1 and 10 percent and to the nearest 5 percent thereafter. Occasionally these ocular estimates were calibrated by using a series of subplots representing 1, 5 and 25 percent canopy cover. Species present within the plot with less than 1 percent canopy cover were noted as "Trace". Other species within the community and not in the plot were noted as "Present" but not included in subsequent data analysis. Three size classes were used for overstory canopy cover by tree species: less than 5 cm, 5 to 15 cm, and greater than 15 cm diameter at 1.37 m in height above the ground (breast height). This separation was designed to give an indication of the relative importance of each size class by species.

A stand table was constructed, consisting of a tally of all live and dead stems by species by 5 cm diameter size class at breast height. Trees between 15 cm and 1.37 m in total height were considered saplings and were distinguished from seedlings. Seedlings and saplings were counted on the whole plot.

Three to five trees of each species with no visible indication of suppression were selected as site trees and measured for stem analysis. Site trees included the full range of diameter and height classes present in the stand rather than being restricted to any particular canopy position. Additional trees were sampled if a skewed diameter distribution suggested age-class differences. Destructive sampling of site trees was used to obtain a measure of total height and stem diameter. Cross-sectional disks were cut at the ground, 0.6 m, 1.37 m, 3.0 m and each additional 2.0 m interval in height to the terminal leader for conifers or base of the main crown for hardwood species.

In addition, some sites were randomly selected for detailed stem mapping prior to plot establishment. On these sites, the same 375 m^2 sample plot was used to obtain azimuth and slope distance from plot center to the center of each stem with staff compass and cloth tape. Mean individual tree canopy diameter was estimated to the nearest decimeter.

Office Methods

All physical site and vegetation data were coded and entered on the

computer. Bedrock, surficial geology and soil series was determined using geologic and soils maps (Rieger *et al.* 1963, Schoephorster 1973, Furbush and Schoephorster 1977, Brown and Kreig 1983). Solar radiation may have a strong influence on species distribution and community composition in these high latitude forests (Dingman and Koutz 1974), consequently the index Latitude of Equivalent Slope (LES) was calculated for each plot based on latitude, azimuth and slope using the FORTRAN program SOLAR2[2].

Taxonomic considerations -- Plant specimens that were difficult to identify in the field were identified in the laboratory. Plant taxonomy followed Hultén (1968) for vascular species and Schofield (1969) and Vitt *et al.* (1988) for nonvascular species. Several species presented problems of identification without complete floral or fruiting material. *Salix alaxensis* and *S. scouleriana* are both shrubs that may reach 5 m in height, have leaves with various shapes but lack diagnostic leaf margins, and vary in leaf pubescence. In general, *S. alaxensis* has dense white felt on the underside of leaves, while *S. scouleriana* is glabrate above and short-pubescent below. All material was treated as *S. scouleriana*.

Feathermosses such as *Hylocomium splendens* are a common feature of boreal conifer communities with closed canopies. Other mosses that accounted for significant ground cover included *Pleurozium schreberi* and *Rhytidiadelphus*

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[2] J.D. Fox, Univ. of Alaska Fairbanks, Department of Forest Science; unpublished.

triquetrus. When other feathermosses were present in only minor amounts (less than one percent cover) and *H. splendens* was abundant, all feathermosses were lumped as *H. splendens*.

Community type classification -- Preliminary association tables (Mueller-Dombois and Ellenberg 1974) were created using canopy coverage values for all herbaceous and shrub species in each plot. Canopy coverage of tree species was not considered at this stage of analysis because herbaceous and shrub layers were assumed to be in greater equilibrium with the environment than tree layers, and because plots were selected on the basis of overstory characteristics. Association tables of undergrowth herbaceous and shrub species were rearranged to emphasize differential species that could be used to differentiate groups of stands. Differential species are those species that have high coverage and fidelity; i.e., they represent a significant portion of the total undergrowth canopy cover within a group of stands and have low constancy in other groups of stands.

The same data set was analyzed with numerical classification; the TWINSPAN algorithm (Hill 1979, Hill *et al.* 1975) provided a hierarchical and divisive classification of the sample plot by species matrix. This algorithm is a reciprocal averaging technique for making successive dichotomous divisions of a data set. The procedure involves maximizing species fidelity in two subsets at different layers of classification.

Groupings of plots by TWINSPAN were compared to groupings of plots arranged within association tables, and inconsistences noted. Plant species having high fidelity and high average cover were noted as indicator species. Individual plots arranged differently by the two methods were included in groups based on the presence and abundance of indicator species. Finally, constancy and average coverage tables for each group were created using selected representative species and coverage values of all tree species.

A dichotomous key to the types was developed based on species dominance. This key was applied to all sample plots and necessary revisions were made to accommodate variations.

A description was prepared for each grouping, including distribution, vegetation and the physical site characteristics. This classification was then used as a basis for characterizing successional relations and stand dynamics.

The community type was used as the basic unit of vegetation classification in this study of forest stand dynamics. Naming the community type required an ability to recognize communities, defined here as a unit of vegetation somewhat homogeneous in all layers and differing from contiguous vegetation in either quantitative or qualitative characteristics (Daubenmire 1968). In contrast, a community type is an abstract grouping of all communities (or stands) based on floristic and structural similarities in both overstory and undergrowth layers. Naming the community type followed the frequently-used convention of a

binomial set with the dominant overstory species separated from the dominant or most diagnostic indicator of the undergrowth by a slash (Mueller-Dombois and Ellenberg 1974). When overstory dominance was shared by two tree species, both were included in the community type name. Community types are units of vegetation which represent the existing structure and composition of communities with no implication of successional status. They differ from habitat types which are units of land supporting or potentially supporting the same climax plant association (Daubenmire 1952, Pfister and Arno 1980, Daubenmire 1989). Once community types are distinguished, successional trends connecting them may then be hypothesized and investigated.

The classification was validated by a technician selecting at random from an independent data set comparable plant community data meeting the same criteria of distribution and overstory composition as this study[3]. The key was then applied to this set of data, and undergrowth community composition and environmental setting compared to the community type descriptions.

Stand physiognomy -- Data from the stand tables, including the number of living and dead stems by tree species and diameter class, were summarized by sample plot and by community type. Quantitative descriptors of stand density included the number of stems per hectare, number of trees per hectare, basal area per hectare and the quadratic mean diameter. Number of trees per

[3] Data on file, Institute of Northern Forestry, Fairbanks, Alaska

hectare was calculated as the total number of live stems greater than 1.37 m in height. Basal area per hectare was calculated as the sum of the basal area of all individual live stems at breast height. Quadratic mean diameter (*QMD*) is the diameter of the tree of average basal area. Because data came from fixed plots, *QMD* is the quadratic mean of the sampled tree diameters computed as:

[1] $$QMD = \sqrt{\Sigma (D^2 \cdot N_1^{-1})}$$

where *QMD* is the quadratic mean diameter in centimeters, *D* is the diameter of each class in centimeters and N_1 is the number of stems in the respective diameter classes. Computationally, *QMD* is related to basal area and stems per hectare by the equation:

[2] $$QMD = \sqrt{BA \cdot (C \cdot N_2)^{-1}}$$

where *BA* is basal area per hectare in square meters, N_2 is the total number of trees per hectare and *C* is the constant 7.854×10^{-5} when diameter classes are in centimeters (Weatherhead *et al.* 1985).

Vertical stand physiognomy was described qualitatively with the foilowing

categories (Oliver and Larson 1990):

- Emergents (or A-stratum)--stems above the highest continuous canopy,
- Upper continuous canopy (or B-stratum)--the grouping of dominant, codominant, intermediate and overtopped crowns forming a single distinct layer of tree canopy,
- Understory (or C-stratum, D-stratum and more)--progressively lower strata beneath the upper continuous canopy,
- Forest floor stratum--trees less than 2 m in height.

Dominant trees are those with at least portions of their crowns at or slightly above the general level of the continuous canopy. These trees receive full sunlight on that portion of the crown extending above the B-stratum. Codominant trees, with the dominant trees, form much of the continuous canopy in any stratum. In the B-stratum, codominant trees receive little direct sunlight from the side of the crown. Intermediate and suppressed or overtopped trees are shorter than the previous two categories and differ in the amount of exposure to the open sky.

Stem locations from stand mapping data were converted to coordinates and dispiayed graphically to represent location and circumference of live crown by species. These figures are presented by community type. Normality of the

frequency distribution of crown diameters in a stand was tested by the statistic *g'* measuring skewness (Puri and Mullen 1980) for species with at least 25 stems.

Reconstruction of stem growth -- A principal intention of this study was the accurate determination of stand and individual stem age, and the changes in stand structure associated with age-class distributions. Cross-sectional disks were first air dried, sanded to clarify ring structure and examined under a binocular microscope. Ring widths were measured to the nearest 0.01 mm with a Bannister-type electronic microcaliper with integral rotary encoder linked to a microcomputer. Two vectors on each cross-sectional disk were measured; one marked as the uphill side while in the field and one opposite. Ring-width series for each disk were cross-dated for consistency.

Total age, based on number of annual rings in the ground-level cross-sectional disk, was obtained for 163 *P. glauca*, 67 *B. papyrifera*, 76 *P. tremuloides*, 4 *P. mariana* and 3 *P. balsamifera*. Mean number of years for establishment, relative to year of establishment of the oldest tree in each stand, were compared among species for each community type with one-way analysis of variance.

Stem growth was reconstructed by plotting tree height-growth and diameter-growth patterns (Larson 1982, Oliver and Larson 1990, Deal *et al.* 1991). Calendar year of pith formation was determined for 1,929 cross-sectional disks,

and height and cumulative diameter inside bark at breast height (1.37 m above the ground) of measured sections plotted against years for sampled trees. The feature of interest in these plots was the slope of the height-growth and diameter-growth curve for different species and for different individuals of the same species on a single site.

Pattems of height-growth for individual trees, age of trees and species composition were considered in describing the age-class structure of each stand. The Society of American Foresters (1971) standardized definitions of age-class structure include:

- All-aged--a forest stand that contains trees of all or almost all age-classes, including those of exploitable age,
- Uneven-aged--a forest stand composed of intermingling trees that differ markedly in age; by convention, a minimum range of 10 to 20 years is generally accepted, though with rotations of less than or equal to 100 years, 25 percent of the rotation age may be the minimum,
- Even-aged--a forest stand composed of trees having no, or relatively small differences in age; by convention, the maximum difference admissible is generally 10 to 20 years, though with rotations of less than or equal to 100 years, differences up to 30 percent of the rotation age may be admissible.

These terms serve a useful purpose for categorizing stands along

conventional concepts of development, but are misleading for stands that have developed slowly after disturbance. Also, the assumption of known rotation age is not always met. In contrast, Oliver (1981) suggested the grouping of trees resulting from a single disturbance event be referred to as a cohort. The age range within a cohort may be as narrow as a single year or as wide as several decades depending on the length of time during which trees invade a site following disturbance. Single-cohort stands contain trees all of which regenerated following a single disturbance event. Multiple-cohort stands contain at least two distinct cohorts from separate and different disturbance events.

Terminology for different stages of development in mixed stands is broad and still evolving. In this study, the following terms taken from Oliver and Larson (1990) were used:

- Stand initiation stage--after disturbance, new individuals and species continue to appear,
- Stem exclusion stage--after a stand initiation stage, new individuals do not appear and some of the existing individuals die. The surviving stems grow larger and express differences in height and diameter. Dominance within the stand may pass from one species to another,
- Understory reinitiation stage--advance regeneration appears in the undergrowth,

- Old growth stage--overstory trees die in an irregular fashion, and some of the understory trees begin growing to the overstory.

Clear distinctions between these terms and their application in individual stands are difficult to make; a portion of one stand may belong to one stage, while another portion of the same stand may belong to another stage. In this study, notes made during field sampling and examination of diameter-class distributions that included mortality by species provided some insight into developmental category.

Estimation of productivity -- The capability of any given site to produce timber is a measure of the site quality. When measured directly as cubic volume per unit area per year, site quality is the same as yield capability, defined as mean annual increment of growing stock attainable in fully stocked natural stands at the age of culmination of mean annual increment (Brickell 1970). Because this method is costly and difficult, indirect methods of estimating site quality are commonly used. One indirect method of estimating site quality is determining height growth, with the assumption that volume-production potential is positively correlated with height growth (Clutter *et al.* 1983). Height growth of a species is not constant through time, however, and height growth curves vary with stand composition and density.

Site index curves are a family of species-specific height development patterns

for dominant trees, generally with the height achieved at some index or base age serving as a reference (Alemdag 1991). Site index curves provide a useful tool to compare relative height growth between different trees on a single site and between trees on different sites because they allow the forward or backward extrapolation of height growth to a common age, referred to as the index age. Site index is a numerical expression of site quality and can be related to growth, yield and management of a stand by association with age (Alemdag 1991). Site index curves are usually developed through stem analysis by sampling in pure stands the dominant and codominant trees that have grown free of suppression. Within the portion of interior Alaska considered within this study, site index curves have been developed for pure, well-stocked stands of mature *P. glauca* (Farr 1967), *B. papyrifera* (Gregory and Haack 1965, Hoyt 1992) and *P. tremuloides* (Gregory and Haack 1965).

Two principal assumptions concerning stand composition and stand density used in the construction and application of existing site index curves are violated when these curves are used to predict growth and yield in mixed stands. First, mixed stands by definition are not pure, and trees in dominant and codominant canopy positions may differ by species. Second, selection of site trees that are vigorous and free of suppression is hampered in mixed stands without any uniform canopy on which to base comparisons. In a stand with overstory dominated by *P. tremuloides*, for example, *P. glauca* may occur

within the continuous canopy and various lower strata. The effect of suppression is not readily apparent. Without knowing exact ages, selection of sample trees can only be based on physical appearance. Methods used to construct site index curves, however, are still useful in modelling tree growth and estimating productivity in mixed stands if measures to eliminate suppressed trees are employed.

Procedures for modelling height growth in this study of mixed stands followed that of constructing polymorphic-nondisjoint site index equations (Zahner 1962, Clutter *et al.* 1983). A family of site index curves in which individual curves are unique in their form and shape are defined as polymorphic-nondisjoint curves. Polymorphic-nondisjoint curves require at least one variable in addition to height and age. In contrast, anamorphic curves follow a guide curve in a constant proportion. Stratification by community type and canopy position relative to competition provided the qualitative variables for polymorphic-nondisjoint curve construction.

Individual *P. glauca* stems were classified into either open-grown and free of competition or stand-grown and suppressed on the basis of growth recorded in annual rings. Changes in conifer cambial growth patterns result in distinguishable stem forms; an open- or free-grown tree has a longer live crown and a stronger taper than a stand-grown tree subjected to competition and side shade (Larson 1963, Oliver and Larson 1990). The usual practice of comparing

diameter growth among different trees is to compare the ring widths of successive years in a series taken at a single vertical position along the bole of the tree, usually at 1.37 m (Fritts 1976, Schweingruber 1985, Kienast and Schwelngruber 1986). This single series is adequate for most purposes of aging the tree but inadequate for revealing cambial growth patterns that are influenced by stand density, crown shape and age.

In this study, radial and longitudinal variation in stem diameter for all cross-sectional disks except the ground section were analyzed with procedures outlined by Duff and Nolan (1953). Basal sections were excluded from this analysis because of distortion in ring width patterns resulting in butt swelling. Graphical representations of cambial growth patterns suggested by Duff and Nolan (1953) incorporate: *i*) the longitudinal position of the internode as sampled by different sections at various heights along the bole, *ii*) the radial position of the internodal ring, and *iii*) the width of the internodal ring. All radial, vertical and diagonal ring width series from the tree base to progressively smaller sections up the stem are a family.

Duff and Nolan (1953) demonstrated that different families of ring width series have characteristic patterns determined by site conditions and stand development, and unpredictable weather conditions. Features determined by stand development serve as indicators of different stand developmental processes. A Type 1 series is ring width measurements plotted such that

contemporary ring widths down the axis of the tree are aligned along a single common time scale of years from origin of internode. For example, the outermost ring, beginning at the top of the tree, is traced down to the base as one series. A second series, shorter than the first series by one year, consists of ring width measurements for the second to the most current ring at the same points of sampling along the stem. This is a two-dimensional representation of the width of the growth layer or a growth layer profile for each year (Fayle 1973). A 50-year old tree, for example, has 50 series.

The intrinsic and systematic factor determining the pattern in Type 1 series is a gradient of nutritive conditions in the cambium caused by crown architecture. Ring-width families from fast-growing trees which are free of competition (Fig. 2) typically exhibit a pattern in all series of an increase in ring width to a maximum followed by a gradual decrease in ring width as the series is traced from the top to the bottom of the tree. The family of Type 1 series in Fig. 2 is for a *P. glauca* which was 18.2 m tall, 17.7 cm in diameter at breast height, and 61 years in total age. For clarity, line type alternates with alternating sequence. After hand-fitting a curve through all series, the general pattern of ring width measurements in this family is an increase in ring width within the first ten year, a peak ring width averaging 2 mm, and then a gradual decline in ring width.

A second *P. glauca* from the same stand has a similar pattern of Type 1 series (Fig. 3). This tree was 17.9 m tall, 19.3 cm in diameter at breast height,

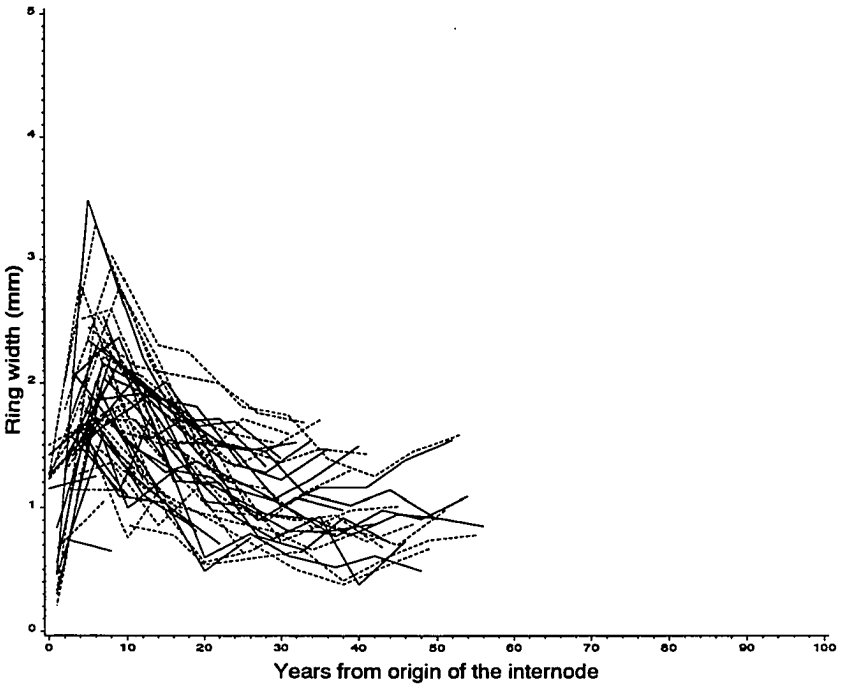

FIG. 2. Family of Type 1 series of ring widths for an open-grown tree, aligned along the year of origin of each internode. The longest series is for the outermost ring. *P. glauca* 3402.

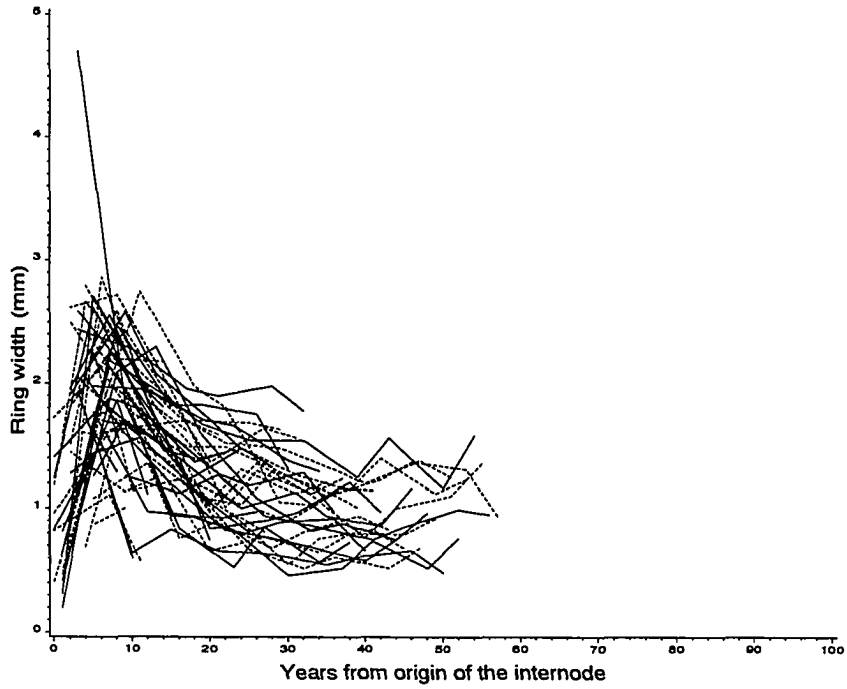

FIG. 3. Family of Type 1 series of ring widths for an open-grown tree, aligned along the year of origin of each internode. The longest series is for the outermost ring. *P. glauca* 3401.

and 63 years in total age. After hand-fitting a curve through all series, the general pattern of ring width measurements for this family is similar to the previous tree: an increase in ring width within the first ten years, a peak ringwidth averaging 2 mm and then a gradual decline in ring width.

In contrast, the pattern of growth for a family of Type 1 series from a tree subjected to suppression differs from the pattern of growth from open-grown trees. In suppressed trees, there is little or no increase in ring width within the early portion of an individual series (Fig. 4). Slow radial growth is expressed by narrow ring widths; hand-fit curves peak at or below 1 mm in ring width. After this peak, however, there is usually a gradual decrease in the ring widths comparable to series from open-grown trees. Typically, ring widths near the base will not be as great as in open-grown trees, therefore stem taper is less and butt swell is absent.

The family of Type 1 series in Fig. 4 is for a *P. glauca* from the same stand as the previous two trees. It was 14.1 m tall, 9.8 cm in diameter at breast height and 63 years in total age. For clarity, line type alternates with alternating series. The general pattern of ring width measurements for all series in this family is an average maximum ring width for each series of 1 mm, and a decrease in ring width with increasing age and distance from the tree crown.

Two other characteristic patterns in Type 1 families are of interest because of their relationship to stand dynamics. The first is for a tree which was initially

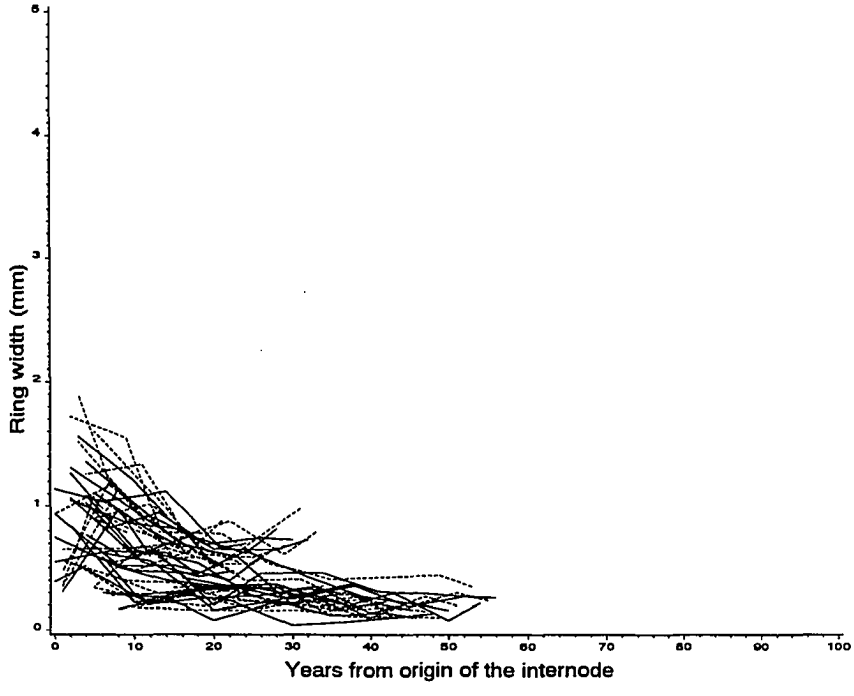

FIG. 4. Family of Type 1 series of ring widths for a suppressed, stand-grown tree, aligned along the year of origin of each internode. The longest series is for the outermost ring. *P. glauca* 3406.

suppressed, but overtopped the competition and became free-growing. individual Type 1 series for outermost rings resemble that of open-grown trees, and shorter series for more internal rings resemble the pattern for stand-grown trees. Conversely, a tree which was initially free-growing but gradually became suppressed because of increasing side shade from neighboring trees has Type 1 series for outermost rings that are narrow and show little increase in early years. More internal rings resemble Type 1 series for open-grown trees.

Duff and Nolan (1953) described a second family of series for radial growth at different heights along the stem. The family of Type 2 series consists of all radial growth series plotted along a scale of common year of formation. One of these series, at 1.37 m in height, is conventionally used in dendrochronology and growth analyses. A tree sampled with ten cross-sectional disks above the ground section has a family of ten Type 2 series. The pattern of radial growth evident in a family of Type 2 series is the systematic distribution of ring growth along the stem. Superimposed on this pattern are extrinsic and random, unpatterned yearly fluctuations. This component involves factors of high variability such as air and soil temperature and water supply.

Three-dimensional representations of annual ring growth are an improvement over the methods of Duff and Nolan (1953) because they integrate temporal and longitudinal growth patterns in a format that both longitudinal and radial sequences are simultaneously displayed, and they reflect the manner in which

the tree has responded to environmental and stand structural changes (Fayle 1973, Clyde and Titus 1987). Clyde and Titus (1987) used diameter increment to describe growth and stem form of *P. glauca* and *P. mariana* in mixed stands from Alberta. Their work suffers, however, from restrictions in the plotting routine which result in three-dimensional graph foregrounds hiding portions of the background. Ring area is a preferred measure because it more closely represents growth along the stem by incorporating the growth necessary to maintain radial increment with increasing circumference (Julin 1984).

Ring area was calculated from annual radial increment for each cross-sectional disk as:

$$[3] \qquad RA_{it} = \pi \left((R_{it})^2 - (R_{i(t-1)})^2 \right)$$

where R_{it} is the radius for disk i at year t based on the summation of mean width of each ring, RA_{it} is ring area for year t and disk i, and $R_{(t-1)} = 0$ when $t = 1$, the first year.

Ring area, age of the ring and height of cross-sectional disks were calculated for 164 *P. glauca*, 71 *P. tremuloides* and 66 *B. papyrifera* stems. Data for a single tree were arrayed as an irregularly spaced grid. From this a regularly spaced grid of ring area and height by consecutive year was interpolated by

using an inverse distance gridding algorithm within the program SURFER[4]. Three-dimensional surface plots of each stem were then plotted with year of ring formation along the x-axis, longitudinal position on the stem along the y-axis, and ring area along the z-axis. When sliced along the x-z plane at different values of y, a family of sequences results which is consistent with Duff and Nolan (1953) Type 2 sequences. The surface plot portrays both longitudinal and radial growth simultaneously, which provides interpretation of stem form.

An example of the three-dimensional surface representation of stem form for a tree with good height and diameter growth shows several characteristic features (Fig. 5). The base of the tree lies along the back baseline, and the apex of the tree migrates from left background to right foreground along the diagonal of pith formation. An inclining slope from the tree apex to the base of the functional crown also migrates with time and tree height. Between this slope and the base of the tree in the background is a relatively flat region representing uniform growth associated with bole expansion below the functional crown. Ring area production resulting in butt swell at the base of the stem is not evident before 1965. Ridges and troughs indicating year-to-year nonuniformity in stem growth occur throughout the profile. A sharp increase in growth is evident beginning in 1982.

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[4] SURFER Ver. 4, distributed by Golden Software, Inc., Golden, Colorado

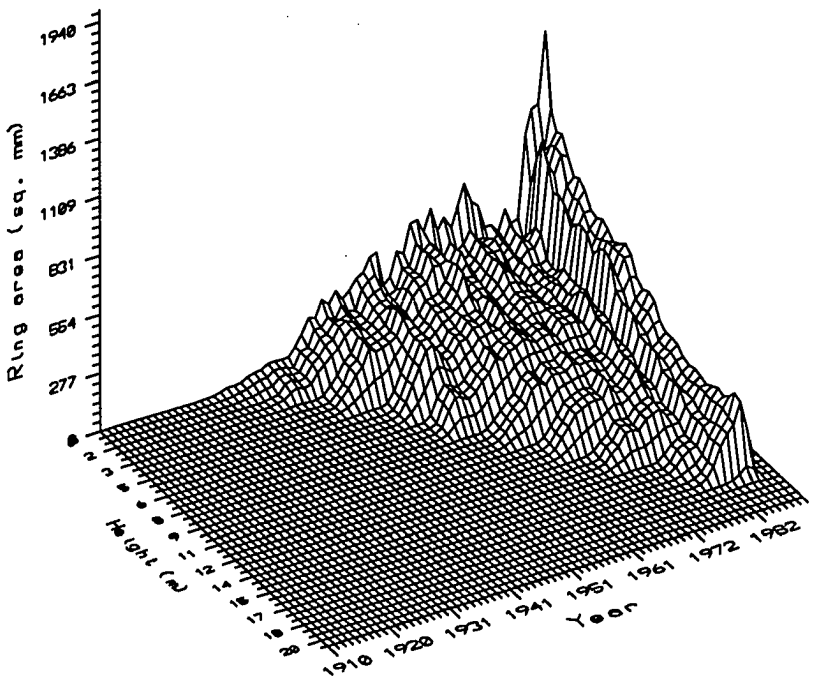


FIG. 5. Example of ring area plotted against position along the bole and calendar year of formation. *Picea glauca* number 606.

The surface plot in Fig. 5 is for a *P. glauca* which was 17.8 m tall and 17.0 cm in diameter at breast height at 61 years of age when sampled. Eleven cross-sectional disks were obtained, 379 ring width-age-height data points were measured, from which 845 additional points were calculated by interpolation, totalling 1,224 non-zero points for creating the surface plot.

Another *P. glauca* from the same stand developed with a sharply contrasting shape of stem (Fig. 6). Ring area gradually increased and remained below about 270 square millimeters per year, with only a slight break in 1982. There was little or no swelling at the base. The relatively flat plateau of ring area increment, between 1945 and 1980 and below 3 m in height, in combination with the gradual taper toward the apex, indicates a small crown that has slowly moved up in height with bole extension. This suppressed tree was 53 years in age, 9.7 m tall and 8.0 cm in diameter at breast height.

Families of Type 1 and Type 2 sequences of ring widths, three-dimensional representations of ring area increment, diameter-growth curves and height-growth curves were examined to characterize individual trees as either open-grown or stand-grown and suppressed. Criteria for distinguishing open-grown trees was: *i*) Type 1 pattern exhibiting an increase in ring width within the first ten year, a peak ring width averaging 2.0 mm and then a gradual decline in ring width; *ii*) Type 2 pattern exhibiting ring width held constant or increasing above 1.0 mm; *iii*) sharp taper from base to tree apex in three-dimensional surface

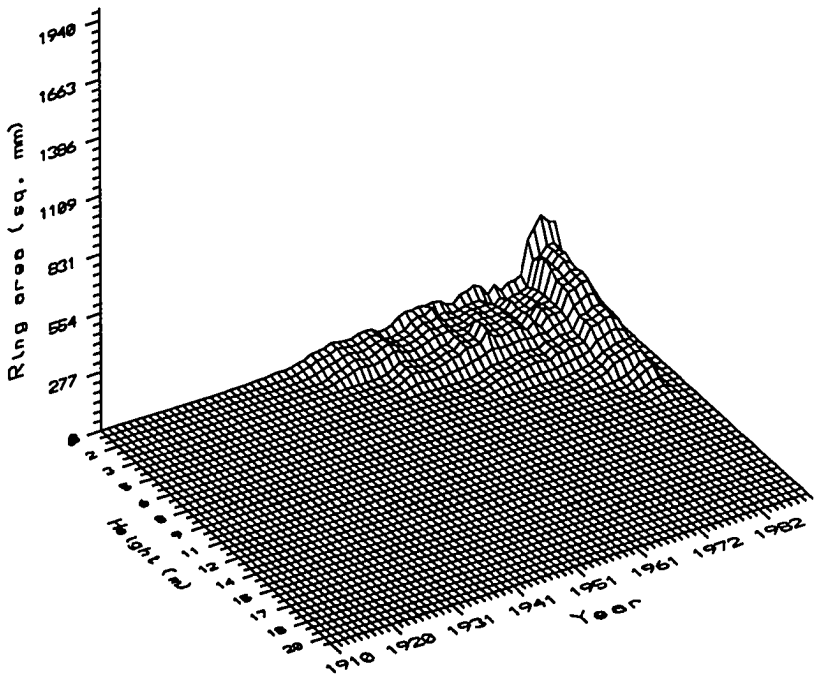


FIG. 6. Example of ring area plotted against position along the bole and calendar year of formation. *Picea glauca* number 607.

representations of ring area; *iv*) sharp taper from pith to outer ring in three dimensional surface representation of ring area; *v*) rate of height growth equal to or greater than neighboring trees of the same species; and *vi*) rate of diameter growth equal to or greater than neighboring trees of the same species. Stem analysis data for open-grown trees were grouped to develop height growth patterns by community type, and represent a measure of site potential. Stem analysis data for suppressed trees were grouped by community type, and represent a measure of natural productivity in the absence of management.

Within each group, nonlinear regression was used to model the relation of tree height growth as a function of total age. The independent variable was total age. Two different nonlinear regression models were fit to the data: the Chapman-Richards function and the negative exponential function. The Chapman-Richards function (Pienaar and Turnbull 1973, Clutter *et al.* 1983, Monserud 1984) produces a sigmoid curve that represents an initial period of slow height growth, a period of steep growth and a period of leveling off associated with cessation of height growth. The general form of the model is:

[4] $$H = \theta_1 [\, 1 - \exp (- \theta_2 A)]^{\theta_3}$$

where H is tree height in meters, A is tree age and θ_1, θ_2 and θ_3 are parameters

to be estimated. Estimates of regression parameters were obtained by using the Gauss-Newton algorithm (SAS Institute, Inc, 1987).

Initial modelling efforts indicated satisfactory fit of the Chapman-Richards model when used with *P. glauca* and most groups of *B. papyrifera*, and a general lack of fit between the model and data for *P. tremuloides* groups. Initial height growth is rapid in *P. tremuloides*, especially when stems are vigorous suckers developed from an existing root system. Height growth was represented more realistically with a negative exponential model. The general form of the negative exponential model is:

$$[5] \qquad H = \theta_1 [\, 1 - \exp (- \theta_2 A)]$$

where H is tree height in meters, A is tree age and θ_1 and θ_2 are parameters to be estimated. Estimates of regression parameters were obtained by using the Gauss-Newton algorithm.

With both Equation 4 and 5, the regression was forced through the origin for zero height when age is also zero. Graphical representations of these nonlinear regressions were constructed, with length of the curve restricted to the total age of the oldest stem in the group.

Site index guide curves for *P. glauca* (Farr 1967) and *B. papyrifera* and *P.*

tremuloides (Gregory and Haack 1965) were compared to height growth models. These site index guide curves provided entry to tabular values of quadratic mean diameter estimated for pure stands.

RESULTS AND DISCUSSION

Community type classification

A total of 53 upland mixed conifer-hardwood forest communities were sampled and classified into five community types (c.t.s): **Populus tremuloides/Arctostaphylos uva-ursi**, **Populus tremuloides/Shepherdia canadensis, Betula papyrifera-Populus tremuloides/Viburnum edule, Betula papyrifera-Populus tremuloides/Alnus crispa** and **Picea glauca-Betula papyrifera/Hylocomium splendens**. Throughout the text and in some tables, c.t. names are also abbreviated, using the standard convention of the first two letters of the generic and specific names; thus **Populus tremuloides/Arctostaphylos uva-ursi** equals **POTR/ARUV**. A key to the c.t.s is presented in appendix C as a tool to assist in using the classification.

Arrangement of c.t.s within the key and within the following discussion progresses along an inferred environmental gradient from the most severe to the least severe, based on species composition and physical characteristics of each sample stand. Manifestation of this inferred environmental gradient is hypothesized as moisture stress.

Briefly, **Populus tremuloides/Arctostaphylos uva-ursi c.t.** is a grouping of relatively warm and dry *Populus tremuloides* stands containing *Arctostaphylos uva-ursi* and other low shrubs in the undergrowth. **Populus tremuloides/**

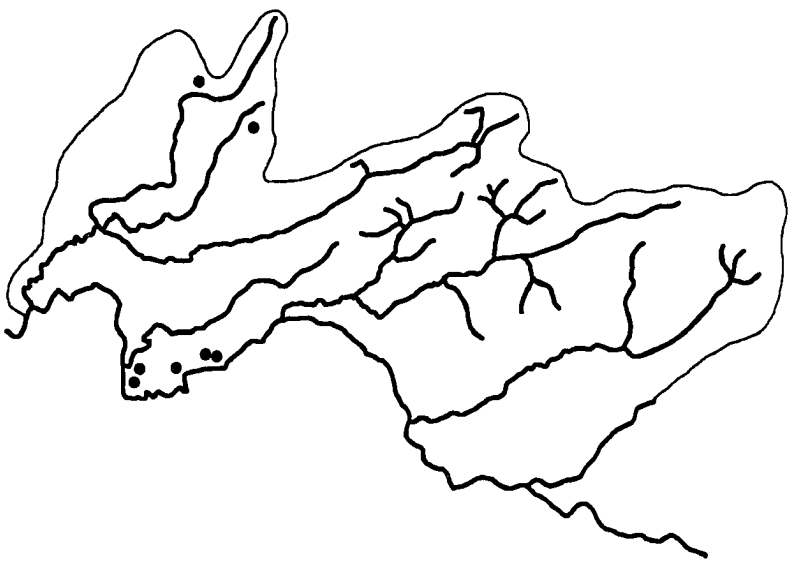
Shepherdia canadensis c.t. is a grouping of *P. tremuloides*-dominated stands on slightly more mesic sites, with an undergrowth consisting of *Shepherdia canadensis* and other tall shrubs. The **Betula papyrifera-Populus tremuloides/Viburnum edule c.t.** and the **Betula papyrifera-Populus tremuloides/Alnus crispa c.t.** include more mesic stands of either *Betula papyrifera* or *P. tremuloides* or a combination of the two, with different undergrowth species compositions. Finally, the **Picea glauca-Betula papyrifera/Hylocomium splendens c.t.** is an aggregration of stands having well-developed moss layers on the forest floor and little shrub cover.

In the following sections, each c.t. is described in terms of general distribution and physical environment, characteristic vegetation composition and structural features, successional relationships of stand development, productivity estimates and finally relationship to other previously-described vegetation units. Dot maps based on Figure 1 indicate known locations of a c.t., and corresponding physical data are summarized in appendix D. A major c.t. covers an extensive area in some drainages. Minor c.t.s may be sporadic throughout the study area but seldom occur as a large unit of vegetation. Constancy and average cover of important plants in each c.t. are summarized in appendix E. Structural features of the c.t. include diameter class distributions by species, vertical stratification, spatial arrangement and stand age, and are summarized in appendix F. Vertical and horizontal arrangement of stems for

representative stands are presented graphically. Patterns of development within each c.t. emphasize stand dynamics within the chronosequence. Reconstruction of height and diameter growth patterns are presented graphically by species for each c.t. Height growth is also compared to predicted height growth in various site index classes. Finally, height growth models with actual data points and both upper and lower bounds of an approximate 95 percent confidence interval for the expected mean are presented in appendix G.

Populus tremuloides/Arctostaphylos uva-ursi c.t.

POTR/ARUV c.t.



Distribution -- **POTR/ARUV c.t.** is a minor type sampled in the extreme western and northern portions of the study area. It is found between 150 and 410 m in elevation (mean = 230 m) on lower and midslopes. It occurs on the warmest and driest sites; exposures range from southeast to south and slope gradients range from 25 to 55 percent (mean = 39 percent). The Latitude of

Equivalent Slope ranges from 37 to 54° (mean = 45°). Slope configuration is either straight or undulating. Adjacent communities on steeper or more southerly aspects are usually non-forested shrub and graminoid steppe.

The **POTR/ARUV c.t.** generally occurs on soils classified as either Lithic or Alfic Cryochrepts, indicating light-colored freely drained soils with limited development which have formed under a cryic temperature regime. Lithic soils are shallow, with a bedrock contact within the upper 50 cm of the soil surface and occur near ridgetops and rock outcrops. Alfic soils are deeper soils that occur on mid and lower slopes and have thin plates in which silicate clays have accumulated. At the family level, these soils are coarse-silty or loamy-skeletal in texture and mixed in mineralogy. Surface organic accumulations within the c.t. are usually less than 3 cm.

Vegetation composition and structure -- *Populus tremuloides* dominates the upper continuous canopy, which generally is between 5 and 15 m in height. Stands are usually dense, with 1,200 to almost 6,000 trees per hectare (mean ± s.e. = 3,558 ± 550) at least 1.37 m in height. *P. tremuloides* accounts for 50 to 70 percent total canopy cover and most of the basal area. *Betula papyrifera*, if present, is only a minor component. *Populus balsamifera* is usually present in the upper continuous canopy in small amounts, often as a codominant or overtopped stem, or as saplings in a C-stratum. Isolated

individual *Picea glauca* may be present in both the upper continuous canopy (B-stratum) and in the undergrowth stratum. Rarely, *P. glauca* may overtop *P. tremuloides* and break out as an emergent.

The diameter-class distribution of living stems (Fig. 7), based on all stems on the site is skewed slightly to the right. Density of all living stems ranges from 1,627 to over 7,000 stems (mean ± s.e. = 4,514 ± 705). Basal area per hectare in square meters (mean = 12.55 ± 2.06) and quadratic mean diameter in centimeters (mean = 7.11 ± 1.07) both indicate small diameters of all stems at least 1.37 m in height. Stands within this c.t. rarely contain stems larger than 15 cm in diameter at breast height. Mortality is concentrated in small diameter *P. tremuloides* with a minor amount of dead *P. glauca*. Taken together, these two frequency distributions clearly resemble the classic reverse "J" or steeply descending monotonic curve characteristic of balanced, all-aged stands.

Stem maps for two stands within this c.t. reflect the high density of stems and the development of small tree crowns found throughout the **POTR/ARUV c.t.** (Fig. 8 and 9). Live crowns on stems greater than 1.37 m in height tend to be clustered together and overlapping, with large canopy gaps providing openings for undergrowth development. *P. tremuloides* in Stand 12 had crowns ranging from 0.6 to 5.0 m in diameter. The frequency distribution was skewed to the right ($g' = 0.71$, $p < 0.01$) because of numerous small stems; mean diameter was 1.8 m, median diameter was 1.7 m and the mode was 1.2 m.

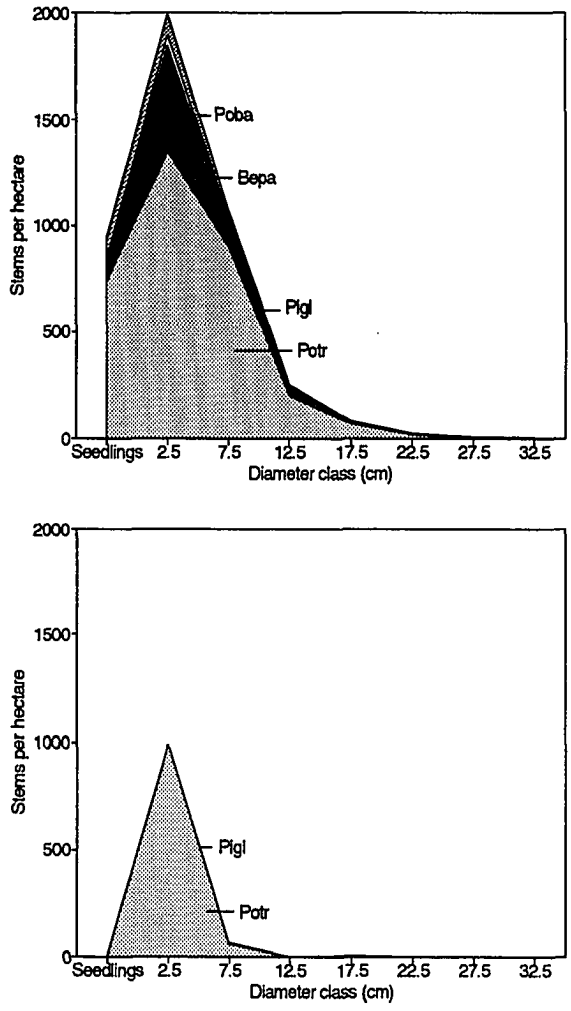


FIG. 7. Frequency distribution of living (above) and dead (below) stems by breast height diameter class and species in the **POTR/ARUV c.t.**

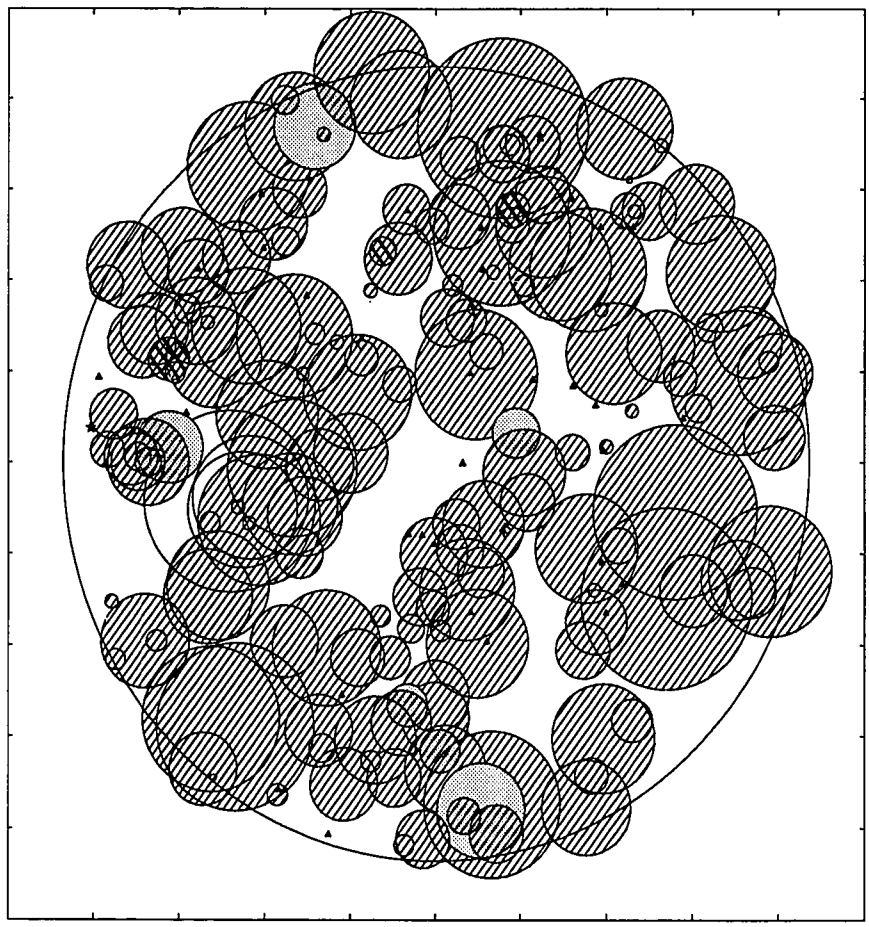


FIG. 8. Crown map for Stand 12 in the **POTR/ARUV c.t.**, indicating spatial arrangement of stems by species. Fill patterns are: ⌀ = *Populus tremuloides*, ▲ = sucker; ⦸ = *Populus balsamifera*, ★ = seedling; ○ = *Betula papyrifera*; ⊙ = *Picea glauca*, ◇ = seedling. Interval of grid is 2.5 meters.

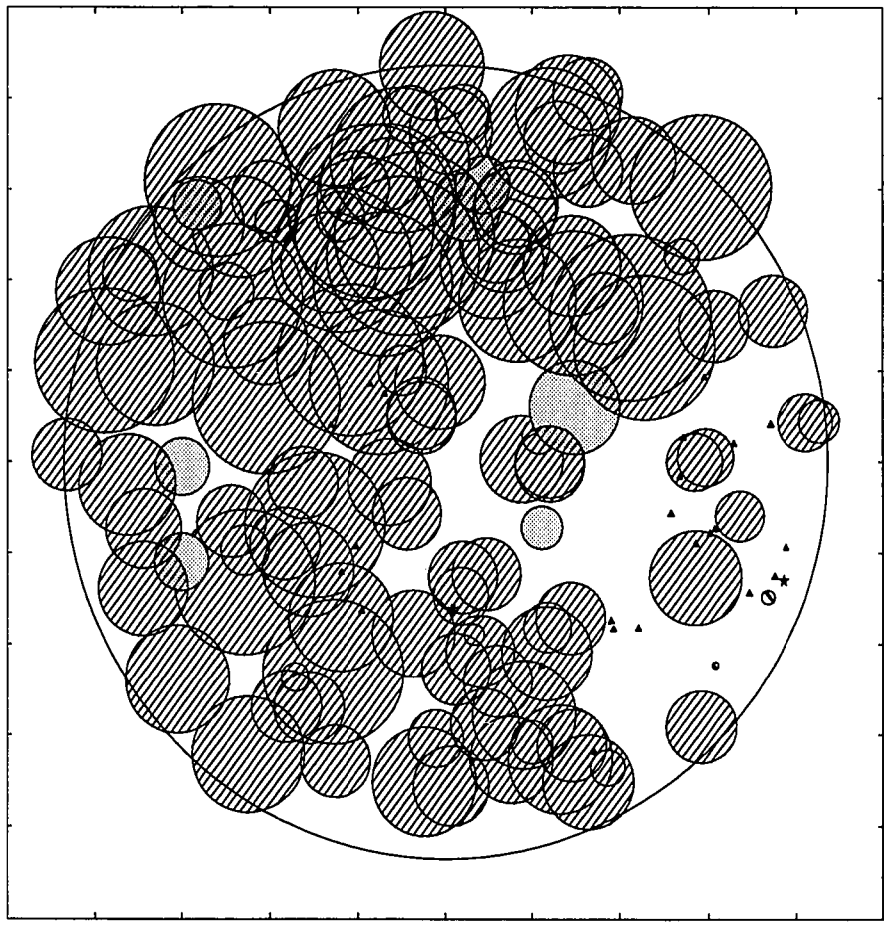


FIG. 9. Crown map for Stand 44 in the **POTR/ARUV c.t.**, indicating spatial arrangement of stems by species. Fill patterns are: ⌀ = *Populus tremuloides*, ▲ = sucker; ⦸ = *Populus balsamifera*, ★ = seedling; ⌾ = *Picea glauca*, ◇ = seedling. Interval of grid is 2.5 meters.

Crown size for the 113 *P. tremuloides* in Stand 44 followed a slightly skewed distribution ($g' = 0.50$, $p < 0.05$) ranging from 0.6 to 4.8 m in diameter with median and mean of 2.4 and 2.6 m, respectively. The few *P. glauca* in this stand had crown diameters with mean, median and mode of 1.6 m. There was no apparent pattern or relationship between the location of *P. glauca* stems and proximity to hardwood stems. In both mapped stands, *P. glauca* occurred close to (or under) the crown of *P. tremuloides* and also occurred in small gaps. Stand 44 contained a dense clumping of *P. tremuloides* in the upper half of the plot, with many suckers in a relatively open portion, suggesting either some microsite influence on root distribution or previous minor disturbance. Corroborating evidence for either explanation was not found.

The undergrowth in the **POTR/ARUV c.t.** is dominated by low shrubs, including *Arctostaphylos uva-ursi, Shepherdia canadensis, Linnaea borealis* and *Viburnum edule*. Canopy cover of *A. uva-ursi* tends to exceed 50 percent in relatively young stands and to decrease gradually with stand age. Large clumps of *Juniperus communis* are sometimes present. Common herbs include *Cnidium cnidiifolium, Galium boreale, Geocaulon lividum, Zigadenus elegans* and *Bromus pumpellianus*. The **POTR/ARUV c.t** is the only type in which the steppe grass *Festuca altaica* was found.

Stand development and productivity -- Totai age was determined for 24 *P. glauca*, 17 *P. tremuloides* and 2 *B. papyrifera*. One *P. glauca* in Stand 21 is a

remnant of a previous stand. The chronosequence of sampled stands in the **POTR/ARUV c.t.** ranges from 44 to 87 total years of age (Table 1). All stands belong to the stem exclusion development stage based on the number of dead stems of small diameter. During this stage some stems have a competitive advantage and are able to rapidly dominate the available growing space, and in so doing may restrict the growth of other stems. Mortality was present in all but the older Stands 11 and 10.

Mean number of years for establishment, relative to age of the oldest tree, is longer for *P. glauca* than for *P. tremuloides* ($p < 0.03$, mean square error = 189.9 with 12 df). *P. tremuloides* becomes established within 11 years of stand-replacing disturbance, and *P. glauca* becomes established within 25 years. There is a consistent pattern of development in this c.t. based on reconstruction of 41 trees (Fig. 10 and 11). *P. tremuloides* acts as a pioneer and regenerates rapidly as suckers from underground root systems following disturbance. Establishment of the *P. tremuloides* component occurs over a period of time averaging 11 years, resulting in almost 4,400 stems per hectare. By the fifth decade, these stands have lost nearly one-third of initial density of *P. tremuloides* stems to mortality through competition. Direct evidence of past fire was noted in some stands, including Stand 49. Other minor disturbances include top breakage from winter snow loading and winds, and defoliation from large aspen tortrix.

Table 1. Age of overstory, sample size (N) and developmental characteristics of sample stands by chronosequence in the **POTR/ARUV c.t.**

Stand	Overstory			Development stage	Additional stems	
	Species[1]	Age	N		Species	Age
21	Potr	44 - 58	3	Early stem exclusion	Bepa	47
					Bepa	46
					Pigl	39
					Pigl	35
12	Potr	50 - 58	2	Early stem exclusion	Pigl	53
					Pigl	43
					Pigl	36
49	Potr	57 - 58	2	Stem exclusion	Pigl	55
					Pigl	44
					Pigl	43
					Pigl	41
					Pigl	40
48	Potr	57 - 65	2	Stem exclusion	Pigl	48
					Pigl	45
					Pigl	39
11	Potr	61 - 66	3	Stem exclusion	Pigl	44
					Pigl	35
44	Potr	68 - 71	3	Stem exclusion	Pigl	63
					Pigl	52
					Pigl	51
					Pigl	40
					Pigl	34
10	Potr	70 - 87	2	Stem exclusion	Pigl	48
					Pigl	45
					Pigl	33

[1] Species codes are: Potr = *Populus tremuloides*, Pigl = *Picea glauca*, Bepa = *Betula papyrifera*

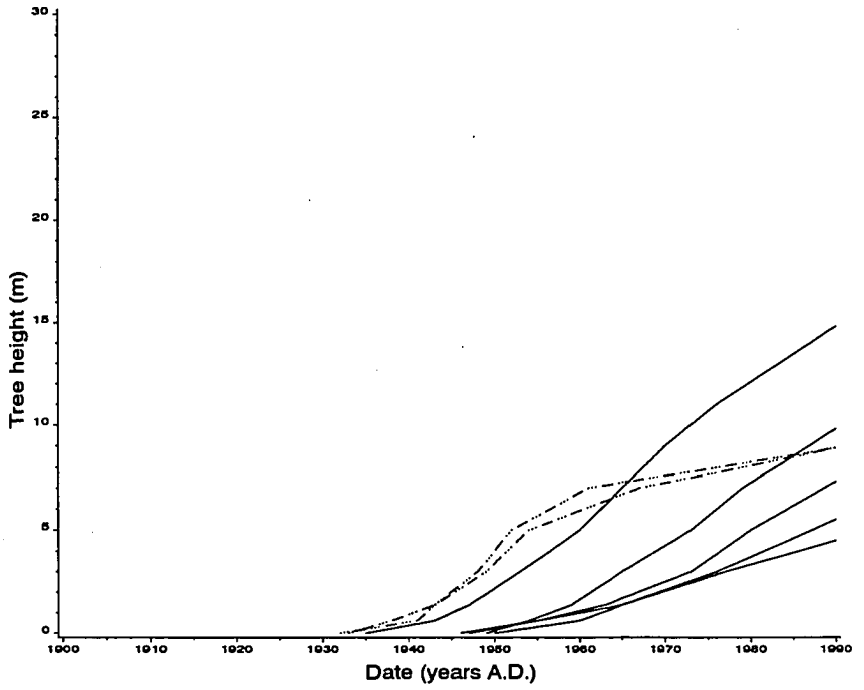


FIG. 10. Development of Stand 49 as a single-cohort, mixed-species stand with a prolonged establishment period. Legend for species composition is: *Populus tremuloides* = ··· — ··· - ; *Picea glauca* = ——— .

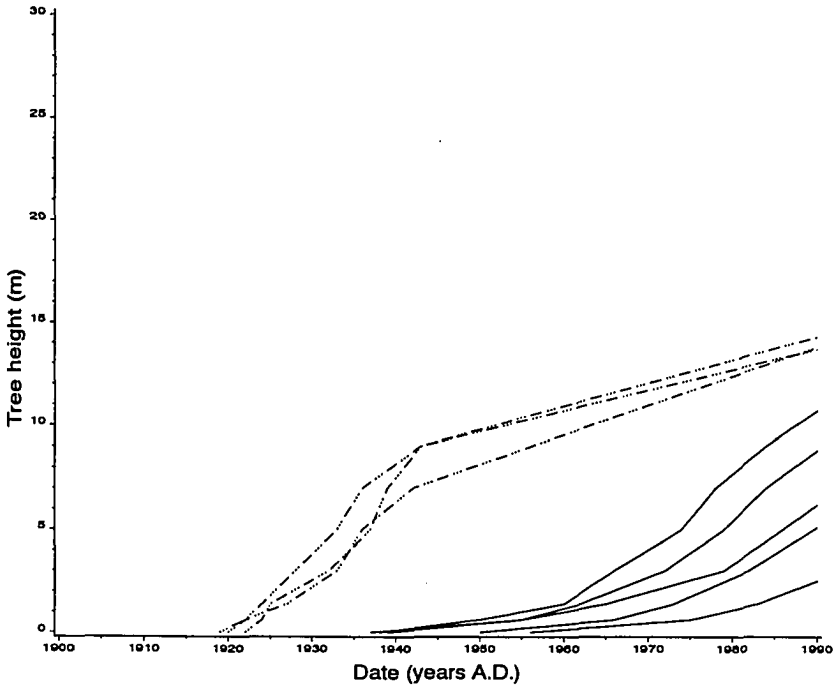


FIG. 11. Development of Stand 44 as a single-cohort, mixed-species stand with a prolonged establishment period. Legend for species composition is: *Populus tremuloides* = ··· — ··· - ; *Picea glauca* = ——— .

Conifers and hardwood species other than *P. tremuloides* have low density in this c.t. From the exterior, stands appear as pure and single-species in composition and of a single cohort in development because scattered conifers are not always apparent until the stand is thoroughly inspected. Occasionally, *B. papyrifera* and *P. glauca* may become established concurrently with *P. tremuloides*, as in Stand 49. More often, *P. glauca* gradually becomes established in a prolonged stand initiation stage lasting several decades. Thick organic layers which often prevent *P. glauca* seedling establishment in other ecosystems are absent in this c.t. A more likely explanation for prolonged conifer establishment is the limited number of years in which seed availability coincides with years of adequate soil moisture during the germination and early establishment period. Soil moisture limitation is inferred from the associated species composition and the site parameters, especially the Latitude of Equivalent Slope. A prolonged invasion of *P. glauca* resulting from the initial stand-replacing disturbance is the only plausible explanation for these mixed stands because physical evidence of repeated disturbance is lacking.

Although the total chronosequence represented by the **POTR/ARUV c.t.** is relatively short, the uniformity in species composition and stand development patterns suggests little additional *P. glauca* establishment. *P. glauca* will continue to grow slowly. *P. tremuloides* is a relatively short-lived species, and stand dynamics during and after *P. tremuloides* canopy deterioration is unclear.

These stands will most likely be replaced under natural fire regimes before complete canopy deterioration occurs. *P. tremuloides* and juvenile *P. glauca* are easily killed by ground fires. Mature *P. glauca* which have developed thick bark are capable of surviving fast-moving ground fires. Most stems are killed, however, if flame fronts follow ladder fuels of low-hanging branches into crowns. It is unlikely these stands will ever be dominated by *P. glauca.*

With the exception of one stand in which the density of *P. glauca* exceeds 3,700 stems per hectare, stands in this c.t. contain *P. glauca* with density below 750 stems per hectare. Rate of *P. glauca* recruitment, based on maximum age of *P. tremuloides* in each stand and observed mortality, averages 19 stems per hectare per year over a 25-year period of recruitment.

The **POTR/ARUV c.t.** is composed of single-cohort, mixed-species stands in which vertical stratification of species is strongly expressed. Height growth and diameter growth of *P. glauca* are severely impacted by the faster height growth of *P. tremuloides.* The single *P. glauca* in Stand 49 (Fig. 10) which became established simultaneously with the hardwoods apparently grew without suppression; after maintaining height growth similar to that of *P. tremuloides*, it broke through the hardwood canopy as an emergent and continued to grow. In 1990, this tree was 14.8 m tall and 19.0 cm in diameter (outside bark) at breast height (Fig 12). Diameter growth at breast height was constant (Fig. 12)

In contrast, the next tallest conifer sampled in Stand 49 became established

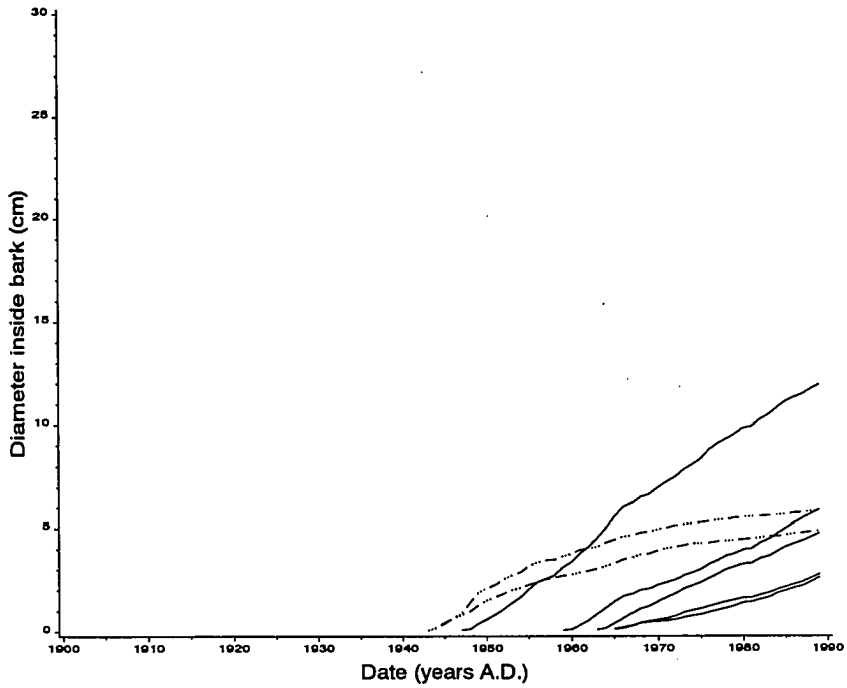


FIG. 12. Cumulative inside bark diameter growth patterns at breast height of representative trees in Stand 49. Legend for species composition is: *Populus tremuloides* = ··· — ··· · ; *Picea glauca* = ——— .

a decade later when the hardwood canopy was several meters tall; this tree grew under suppressed conditions, was beginning to emerge from the 8.9 m tall hardwood canopy in 1990, and was 9.8 m in height and 10 cm in diameter at breast height. Additional sample trees from Stand 49 reflect a greater degree of suppression as expressed by radial growth.

Eight *P. glauca* sampled for stem analysis were open-grown and free of competition, and were used to construct a model depicting mean height growth (Table 2 and Fig. 13). A second group of 15 trees was used to model the

Table 2. Species, number of sample trees, model parameters and error terms used in nonlinear regression models of height growth in the **POTR/ARUV c.t.**

Species[1]	N[2]	Model[3]	DF[4]	MSR	MSE	Estimated Parameters		ASE[5]
Open Pigl	8	CR	59	603.71	1.37	θ_1 =	36.6765	35.293
						θ_2 =	0.0174	0.017
						θ_3 =	2.1591	0.695
Supp Pigl	15	CR	78	256.91	0.51	θ_1 =	41.8356	72.408
						θ_2 =	0.0122	0.017
						θ_3 =	2.2772	0.748
Potr	14	NE	74	1369.91	3.12	θ_1 =	45.0983	26.627
						θ_2 =	0.0053	0.004

[1] Species codes are: Open Pigl = Open-grown *Picea glauca*; Supp Pigl = Suppressed *Picea glauca*; Potr = *Populus tremuloides*
[2] Number of trees in sampie
[3] CR = Chapman-Richards; NE = Negative Exponential
[4] Uncorrected total degrees of freedom
[5] Asymptotic standard error

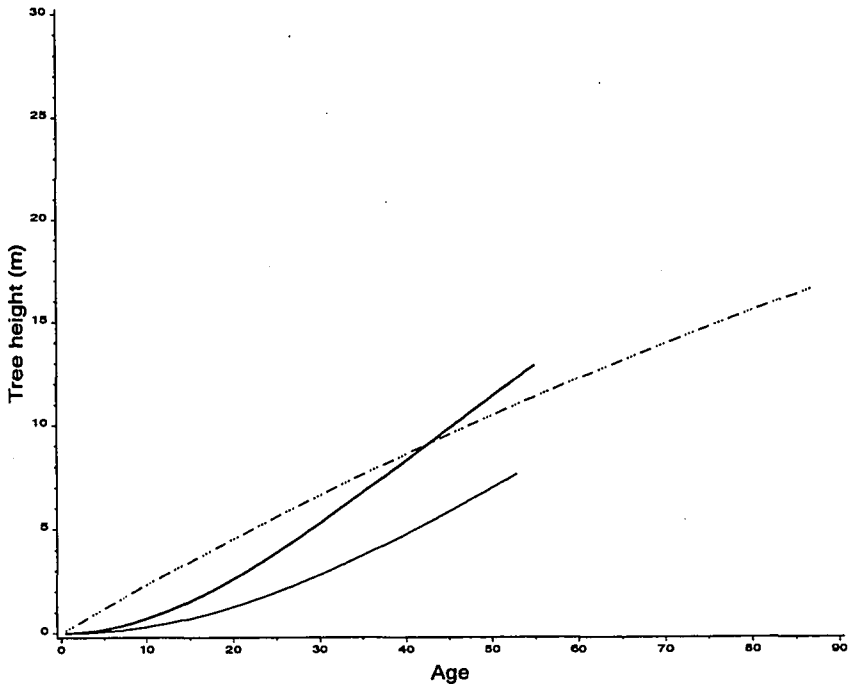


FIG. 13. Mean height growth in the **POTR/ARUV c.t.** Legend for species composition is: *Populus tremuloides* = ··· — ··· - ; Open-grown *Picea glauca* = ——— ; Suppressed *Picea glauca* = ——— .

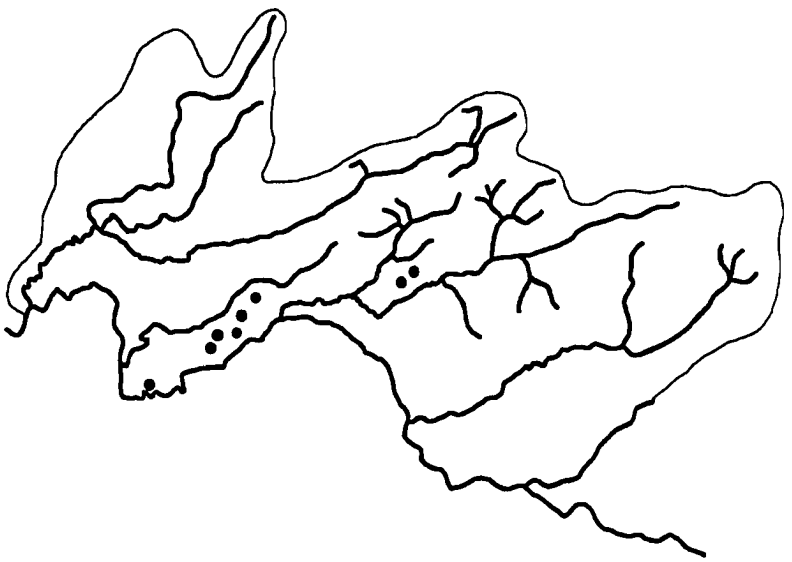
height growth of suppressed *P. glauca*. *P. glauca* growing free of competition in the **POTR/ARUV c.t.** reach a height of 1.37 m in slightly less than 15 years, while *P. glauca* experiencing competition reach the same height in 21 years. After 50 years, open-growing *P. glauca* are almost 12 m in height, and suppressed *P. glauca* are slightly more than 7 m. In contrast, *P. tremuloides* has a greater rate of growth initially, reaching breast height in six years. It will be slightly more than 10 m in height after 50 years. Direct comparison between species should be made with care; these height growth curves predict the rate of growth of individual species after establishment. In this c.t., establishment of *P. glauca* and hardwoods is not concurrent.

Other studies -- **POTR/ARUV c.t.** is similar in name to the **Aspen-white spruce/Arctostaphylos uva-ursi** vegetation unit listed by Viereck (1975) as representing a stage of succession in which *P. glauca* replaces the deciduous trees. No detailed description is provided. Yarie (1983) described **Populus tremuloides/Salix/Arctostaphylos uva-ursi** and **Populus tremuloides-Picea glauca/Salix/Arctostaphylos uva-ursi** communities in the Porcupine River drainage of northeastern Alaska which differ in site characteristics and species composition. Viereck *et al.* (1983) described a single stand dominated by *Populus tremuloides* and *Shepherdia canadensis* that has many affinities to the **POTR/ARUV c.t.**; their stand contained only a single tree species, however, and is ecotonal between dense forests and open steppe. Stanek and Orloci

(1987) described a **Populus-Arctostaphylos-Shepherdia** vegetation type on volcanic ash in the Yukon Territory that has some affinity with this **POTR/ARUV** and the **POTR/SHCA c.t.** Oswald and Brown (1986) describe a **Populus tremuloides/Arctosyaphylos** type that occurs on dry sites with well-drained glaciofluvial and eolian soils in the Lake Laberge ecoregion of the Yukon Territory. Their type is considered successional to *P. glauca*-dominated forests, however, and is therefore distinct rather than disjunct. The **POTR/ARUV c.t.** as described here represents a new Level V type in the Closed Quaking Aspen Forest (I.B.1.e.) of Viereck *et al.* (in prep.).

Populus tremuloides/Shepherdia canadensis c.t.

POTR/SHCA c.t.



Distribution -- **POTR/SHCA c.t.** is a minor type sampled in the central portion of the study area on sites between 170 and 300 m in elevation (mean = 230 m). It occurs on various aspects from southeast through southwest with gentle to moderately steep slopes (mean = 17 percent). The Latitude of Equivalent Slope ranges from 47 to 62° (mean = 57°). This type can occur on the full

range of slope positions, including upper slopes, lower slopes and benches. Configurations include all but concave terrain.

The **POTR/SHCA c.t.** generally occurs on soils classified as Alfic Cryochrepts, indicating light-colored freely drained soils with limited development which have formed under a cryic temperature regime. Soil development is manifested in the transportation and accumulation of silicate clays. Some soils supporting this c.t. may be classified as Aeric Cryaquepts, indicating saturation of the soil profile during some period of the year and the potential for permafrost deep in the profile. These soils are grayer than those classified as Cryochrepts. At the family level, these soils are coarse-silty in texture and mixed in mineralogy. Surface organic accumulations within the c.t. are similar to those in the **POTR/ARUV c.t.**

Vegetation composition and structure -- *Populus tremuloides* dominates the upper continuous canopy in the **POTR/SHCA c.t.**, the top of which may be from 14 to 22 m above the ground. Overstories range from 50 to 75 percent canopy cover. Both *Betula papyrifera* and *Populus balsamifera* are sometimes present in the B-stratum as scattered codominant or intermediates. *Picea glauca* is most often present as saplings in a lower stratum. Presence of *Picea mariana* is sparse and accidental.

The frequency distribution of stems by diameter classes is skewed to the right because of a preponderance of small stem diameters (Fig. 14). Density of

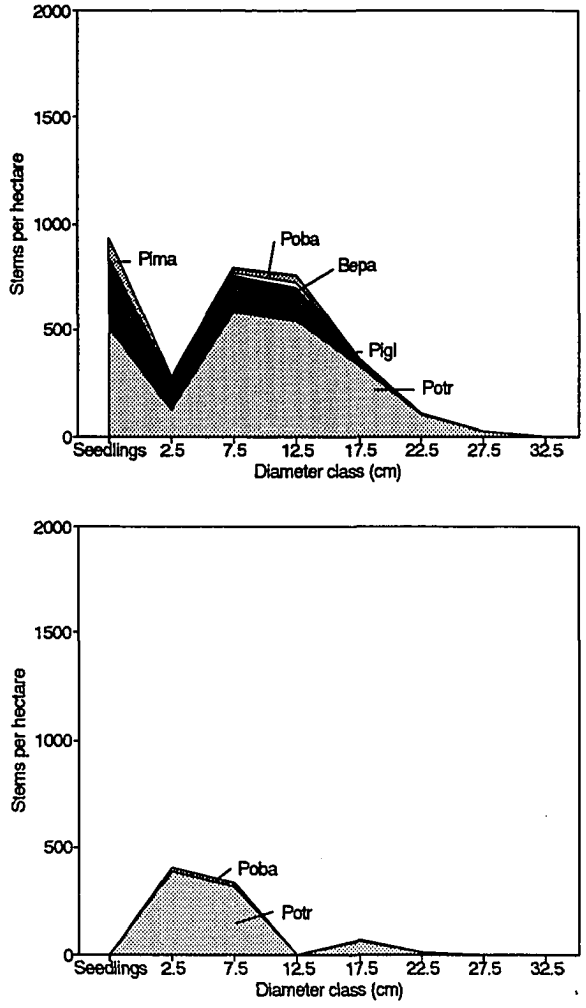


FIG. 14. Frequency distribution of living (above) and dead (below) stems by breast height diameter class and species in the **POTR/SHCA c.t.**

all living stems ranges from more than 1,500 to almost 6,000 stems per hectare (mean ± s.e. = 3,263 ± 479). Density of living trees at least 1.37 m tall ranges from more than 1,200 to over 3,500 trees per hectare (mean = 2,327 ± 242). Distribution of *P. tremuloides* is somewhat bell-shaped, peaking between 5 and 15 cm in diameter. Many stems in the smaller diameter classes, however, have been lost to mortality through competition. *P. glauca* has an even or uniform frequency distribution in the small diameter classes. Both *P. balsamifera* and *B. papyrifera* appear as truncated distributions in the middle size classes suggesting their growth has occurred simultaneously with *P. tremuloides*. Mortality of *P. balsamifera* tends to occur more frequently in the smaller diameter classes.

P. tremuloides accounts for more than 80 percent of the basal area of living stems greater than 1.37 m tall. Basal area per hectare in square meters (mean = 27.22 ± 3.1) and quadratic mean diameter in centimeters (mean = 12.44 ± 0.88), based on all species, indicate the larger diameter *P. tremuloides* stems in this c.t. compared to the **POTR/ARUV c.t.**

Stem maps of two stands within this c.t. indicate different canopy conditions (Fig. 15 and 16). Stand 19 contained over 2,200 trees per hectare, close to the mean for this c.t. Individual *P. tremuloides* crowns were tightly clumped and overlapping. Crown size followed a frequency distribution skewed to the left ($g' = -0.93$, $p < 0.01$) ranging from 0.2 to 6.0 m in diameter, with mean, median

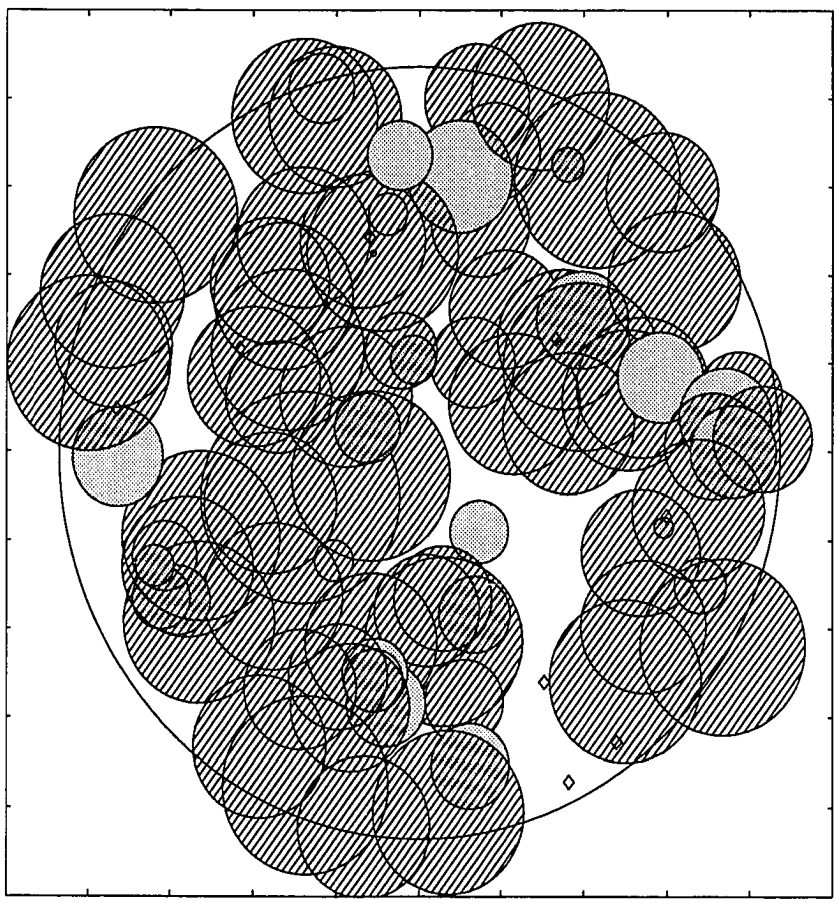


FIG. 15. Crown map for Stand 19 in the **POTR/SHCA c.t.**, indicating spatial arrangement of stems by species. Fill patterns are: ⊘ = *Populus tremuloides*; ○ = *Picea glauca*, ◇ = seedling. Interval of grid is 2.5 meters.

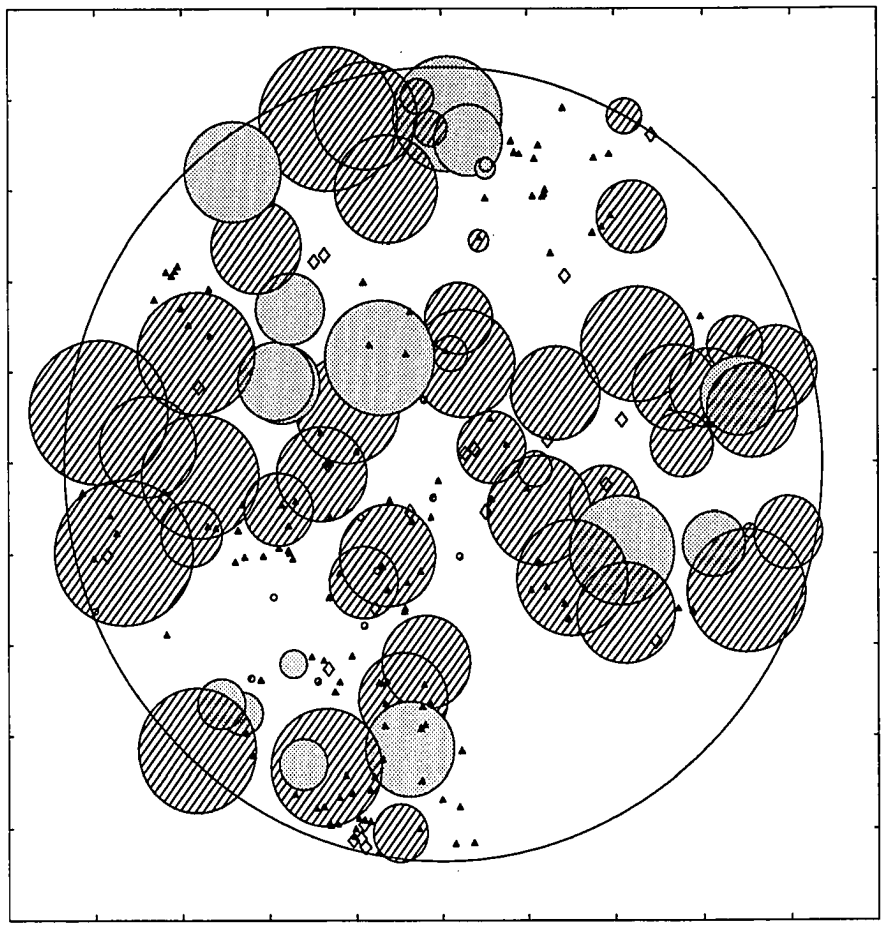


FIG. 16. Crown map for Stand 8 in the **POTR/SHCA c.t.**, indicating spatial arrangement of stems by species. Fill patterns are: ⊘ = *Populus tremuloides*, ▲ = sucker; ⊙ = *Picea glauca*, ◇ = seedling. Interval of grid is 2.5 meters.

and mode between 3.7 and 4.0 m in diameter. *P. glauca* stems were dispersed throughout the stand. Mean, median and mode of *P. glauca* crown diameter was 2.0 m. Total canopy cover of all trees in the upper continuous canopy within Stand 19 was estimated at 75 percent. The number of seedlings or suckers was notably small. Stand 8 was composed of fewer trees; both *P. tremuloides* and *P. glauca* crowns averaged about 2.0 m in diameter. The largest *P. glauca* crown was 3.2 m in diameter. Clustering of both *P. glauca* and *P. tremuloides* seedlings and suckers was apparent. This stand also contained large canopy gaps devoid of trees. Total canopy cover of all trees In the upper continuous canopy of Stand 8 was estimated at 50 percent.

The undergrowth in the **POTR/SHCA c.t.** is characteristically shrubby, with a tall shrub stratum consisting of *Rosa acicularis, Shepherdia canadensis* and *Viburnum edule* and a low shrub stratum consisting of *Linnaea borealis.* Cover of forbs is usually scarce, and includes *Epilobium angustifolium, Galium boreale* and *Geocaulon lividum.*

Stand development and productivity -- Total age was determined for 31 *P. glauca,* 2 *B. papyrifera,* 22 *P. tremuloides* and 3 *P. balsamifera.* The chronosequence of sampled stands in the **POTR/SHCA c.t.** extends from 63 to 93 total years of age (Table 3). Of the eight stands sampled, all but one belonged to the stem exclusion development stage based on the number of dead stems with small diameters. In this development stage some stems

Table 3. Age of overstory, sample size (N) and developmental characteristics of sample stands by chronosequence in the **POTR/SHCA c.t.**

Stand	Overstory			Development stage	Additional stems	
	Species[1]	Age	N		Species	Age
35	Potr	63 - 66	4	Stem exclusion	Bepa	64
					Bepa	63
					Pigl	60
					Pigl	49
					Pigl	49
					Pigl	48
					Poba	69
					Poba	64
					Poba	63
9	Potr	68 - 72	2	Stem exclusion	Pigl	52
					Pigl	50
					Pigl	42
					Pigl	41
36	Potr	71 - 72	5	Stem exclusion	Pigl	45
					Pigl	44
					Pigl	37
					Pigl	37
24	Potr	73 - 75	2	Stem exclusion	Pigl	57
					Pigl	53
					Pigl	49
45	Potr	63 - 78	3	Stem exclusion	Pigl	74
					Pigl	73
					Pigl	71

(Cont.)

Stand	Overstory			Development stage	Additional stems	
	Species[1]	Age	N		Species	Age
14	Potr	85 - 86	3	Stem exclusion	Pigl	72
					Pigl	72
					Pigl	67
19	Bepa	85 - 86	2	Late stem exclusion	Pigl	73
					Pigl	72
					Pigl	72
					Pigl	27
8	Potr	83 - 93	2	Understory reinitiation	Pigl	74
					Pigl	70
					Pigl	62
					Pigl	57
					Pigl	37

[1] Species codes are: Potr = *Populus tremuloides*, Pigl = *Picea glauca*, Bepa = *Betula papyrifera*, Poba = *Populus balsamifera*

express competitive advantage over their neighbors through greater height and diameter growth and dominance of growing space. Neighboring stems that suffer competition have decreased diameter and sometimes height growth and develop small crowns with little photosynthetic potential; stems with poor vigor may die. Mortality in the smaller diameter classes occurred in the eight stands.

The oldest stand sampled in this c.t. represents the reinitiation stage, in which advance regeneration becomes established in the undergrowth. Designation of Stand 8 as a reinitiation stage was based on a bimodal

frequency distribution of both living *P. tremuloides* and *P. glauca*. The number of *P. tremuloides* and *P. glauca* stems was greatest in the seedling and small sapling diameter classes, decreased to a low in the 5 to 10 cm diameter class, and then increased in the larger diameter classes. In this same stand, mortality of *P. tremuloides* occurred over a bell-shaped frequency distribution peaking in the 5 to 10 cm diameter class.

Stand development, based on reconstruction of 55 trees, followed a consistent pattern throughout sampled stands within this c.t. The development pattern is based on different establishment and growth patterns of the component species. Like the **POTR/ARUV c.t.**, stand development in this c.t begins with different species establishing as a single cohort over an extended period of time (Fig. 17 and 18). During an establishment period that averages two years, *P. tremuloides* colonizes these sites with at least 3,000 stems per hectare. About 25 percent of these are lost as mortality during the stem exclusion stage of development. Occasionally, *B. papyrifera* may seed in and become established simultaneously with *P. tremuloides*. Mean number of years for establishment of *P. glauca* is longer than for hardwoods ($p < 0.01$, mean square error = 36.51 with 14 df); *P. glauca* established within 23 years. Rate of *P. glauca* recruitment, based on maximum age of the hardwoods in each stand, averages 37 stems per hectare per year over a 30-year period of recruitment.

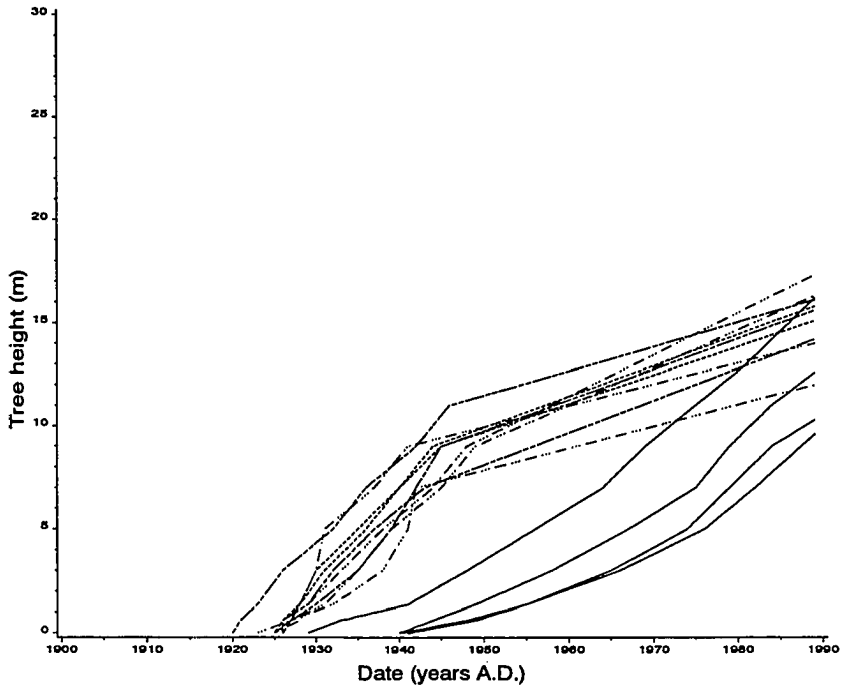


FIG. 17. Development of Stand 35 as a single-cohort, mixed-species stand with a prolonged establishment period. Legend for species composition is: *Populus tremuloides* = ··· — ··· - ; *Populus balsamifera* = ------ ; *Betula papyrifera* = -------- ; *Picea glauca* = ——— .

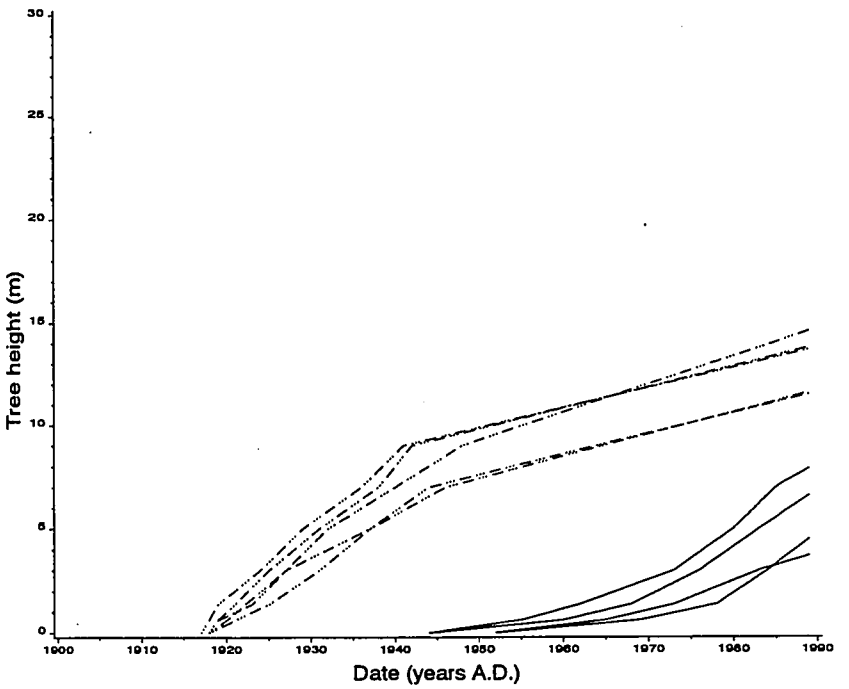


FIG. 18. Development of Stand 36 as a single-cohort, mixed-species stand with a prolonged establishment period. Legend for species composition is: *Populus tremuloides* = ··· — ··· · ; *Picea glauca* = ——— .

This is almost twice the rate of recruitment of the **POTR/ARUV c.t.** No *P. glauca* mortality was noted.

Patterns of development for *P. tremuloides* in the **POTR/SHCA c.t.**, following establishment, are similar to those in the **POTR/ARUV c.t.** Little vertical stratification occurs within the *P. tremuloides* canopy. Dominance of individual stems is reflected, however, in horizontal stratification, resulting in a wide range of diameters within a single stand. In Stand 36, four *P. tremuloides* differed in total height by 3.1 m, in diameter outside the bark by 10.5 cm and in diameter inside the bark by 6 cm (Fig. 19).

Twelve *P. glauca* sampled for stem analysis were open-grown and free of competition in the **POTR/SHCA c.t.**, and were used to construct a model depicting mean height growth (Table 4 and Fig. 20). A second group of 13 trees was used to model the height growth of suppressed *P. glauca*. *P. glauca* growing free of competition in this c.t. reach a height of 1.37 m in slightly less than 16 years, while *P. glauca* experiencing competition may require 21 years to reach the same height, similar to initial growth in the **POTR/ARUV c.t.** After 50 years, open-growing *P. glauca* are just over 10 m in height and suppressed *P. glauca* are almost 8 m. *P. tremuloides* has a faster rate of growth initially, reaching breast height in three years and slightly more than 13 m in height after 50 years. Direct comparison of height growth should be made with caution; these height growth curves predict the rate of growth of individual species after

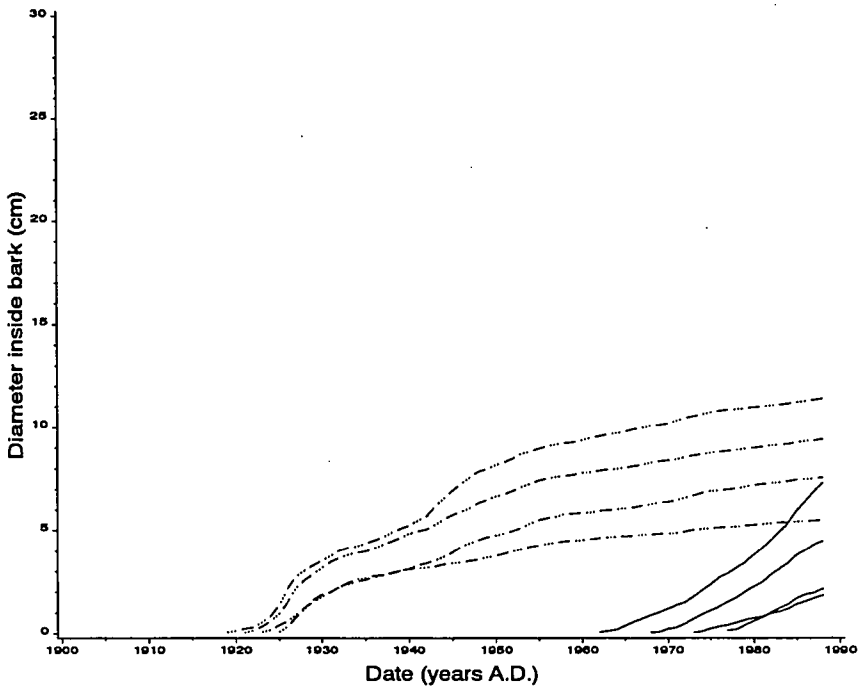


FIG. 19. Cumulative inside bark diameter growth patterns at breast height of representative trees in Stand 36. Legend for species composition is: *Populus tremuloides* = ··· — ··· · ; *Picea glauca* = ——— .

Table 4. Species, number of sample trees, model parameters and error terms used in nonlinear regression models of height growth in the **POTR/SHCA c.t.**

Species[1]	N[2]	Model[3]	DF[4]	MSR	MSE	Estimated Parameters		ASE[5]
Open Pigl	12	CR	102	1701.45	2.48	θ_1 =	19.7714	3.643
						θ_2 =	0.0307	0.009
						θ_3 =	2.7493	0.683
Supp Pigl	13	CR	90	854.51	2.20	θ_1 =	11.6143	1.246
						0_2 =	0.0536	0.013
						θ_3 =	5.3569	1.989
Potr	19	NE	114	3745.20	2.37	θ_1 =	29.1986	3.059
						θ_2 =	0.0123	0.002

[1] Species codes are: Open Pigl = Open-grown *Picea glauca*; Supp Pigl = Suppressed *Picea glauca*; Potr = *Populus tremuloides*
[2] Number of trees in sample
[3] CR = Chapman-Richards; NE = Negative Exponential
[4] Uncorrected total degrees of freedom
[5] Asymptotic standard error

establishment. In this c.t., establishment of *P. glauca* and hardwoods is not concurrent.

Other studies -- No other studies have described the **POTR/SHCA c.t.** Stanek and Orloci (1987) described a **Populus-Arctostaphylos-Shepherdia** vegetation type on volcanic ash in the Yukon Territory that has some affinity with this **POTR/SHCA** and the **POTR/ARUV c.t.** Oswald and Brown (1986)

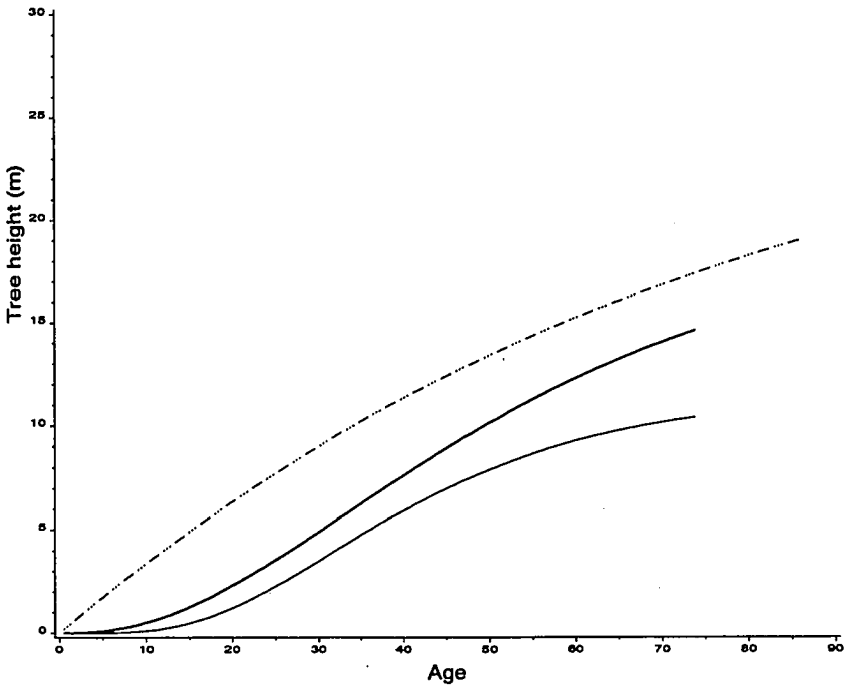


FIG. 20. Mean height growth in the **POTR/SHCA c.t.** Legend for species composition is: *Populus tremuloides* = ··· — ··· - ; Open-grown *Picea glauca* = ——— ; Suppressed *Picea glauca* = ——— .

describe a **Populus tremuloides/Arctosyaphylos** type that occurs on moist to mesic sites with morainal or eolian soils in the Lake Laberge ecoregion of the Yukon Territory. Their type is considered successional to *P. glauca*-dominated forests, however, and is therefore distinct rather than disjunct. The **POTR/SHCA c.t.** as described here represents a new Level V type in the Closed Quaking Aspen-Spruce Forest (I.C.1.d.) of Viereck *et al.* (in prep.).

Betula papyrifera-Populus tremuloides/Viburnum edule c.t.

BEPA-POTR/VIED c.t.

Distribution -- The **BEPA-POTR/VIED c.t.** is a major type sampled throughout the study area between 150 and 450 m (mean = 272 m) in elevation. It typically occurs on mid to upper slopes with gentle to moderately steep gradients (mean = 17 percent) and straight slope configuration or on flat to gentle benches. It occurs on all but northern aspects; the Latitude of

Equivalent Slope ranges from 45 to 65° (mean = 58°).

Throughout most of the study area, the **BEPA-POTR/VIED c.t.** occurs on soils classified as Alfic Cryochrepts, indicating light-colored freely drained soils with limited development which have formed under a cryic temperature regime. These soils have thin layers of silicate clays which have accumulated within the profile from weathering of the micaceous loess. At the family level, these soils are classified as loamy-skeletal. Exceptions to this dominant type include colder and wetter soils on toeslopes or within the influence of upland streams. Under these more extreme conditions, soils are classified as either Pergelic or Aeric Cryaquepts, indicating saturation of the soil profile during some period of the year and the potential for permafrost deep in the profile. Throughout this c.t., surface organic accumulations are 3 to 5 cm thick.

Vegetation composition and structure -- The **BEPA-POTR/VIED c.t.** is a diverse assemblage of species consisting of several distinct strata. The upper continuous canopy (B-stratum) consists of either *Populus tremuloides* or *Betula papyrifera* or a combination of the two, is relatively dense and ranges from 12 to 25 m in height. *Populus balsamifera* may also occur as a codominant but contributes little canopy cover. *Picea glauca* may occur in a dominant, codominant or intermediate position within the B-stratum or a lower C-stratum, or as an emergent above the B-stratum. Density of all trees at least 1.37 m in

height ranges from 773 to over 6,400 stems per hectare (mean ± s.e. = 2,741 ± 426).

The diameter-class distribution of all stems contains differences by species (Fig. 21). Both living and dead *B. papyrifera* have a normal or bell-shaped frequency distribution. The frequency distribution of *P. tremuloides* is also somewhat normal, although mortality is greatest in the 0 to 5 and 5 to 10 cm classes. *P. glauca* occurs most often as small-diameter stems. Density of all stems is similar to the **POTR/SHCA c.t.** (mean = 3,436 ± 619). Basal area per hectare in square meters (mean = 26.21 ± 2.14) of trees at least 1.37 m in height is similar to that in the **POTR/SHCA c.t.** *B. papyrifera* accounts for approximately 37 percent, *P. tremuloides* accounts for about 32 percent and *P. glauca* accounts for about 15 percent of the basal area. The remaining 16 percent is comprised of *P. balsamifera* and *P. mariana*. Quadratic mean diameter in centimeters (mean = 12.4 ± 1.09) is similar to that of the **POTR/SHCA c.t.**

Stem maps of three stands portray the variation in crown structure and spatial arrangement of stems in this c.t. Stand 5 contained more than 9,000 live stems per hectare, of which 2,320 were live *B. papyrifera* at least 1.37 m in height (Fig. 22). These trees had crowns ranging from 0.2 to 5.0 m in diameter. Mean crown diameter was 2.6 m, median was 2.3 m and the mode was 2 m. *B. papyrifera* crown diameters followed a normal distribution

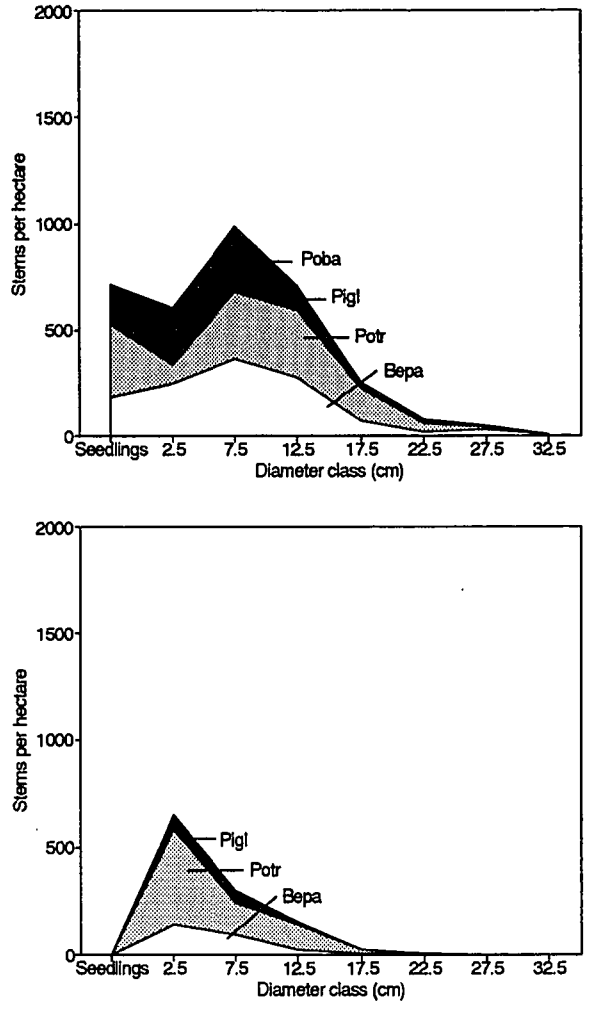


FIG. 21. Frequency distribution of living (above) and dead (below) stems by breast height diameter class and species in the **BEPA-POTR/VIED c.t.**

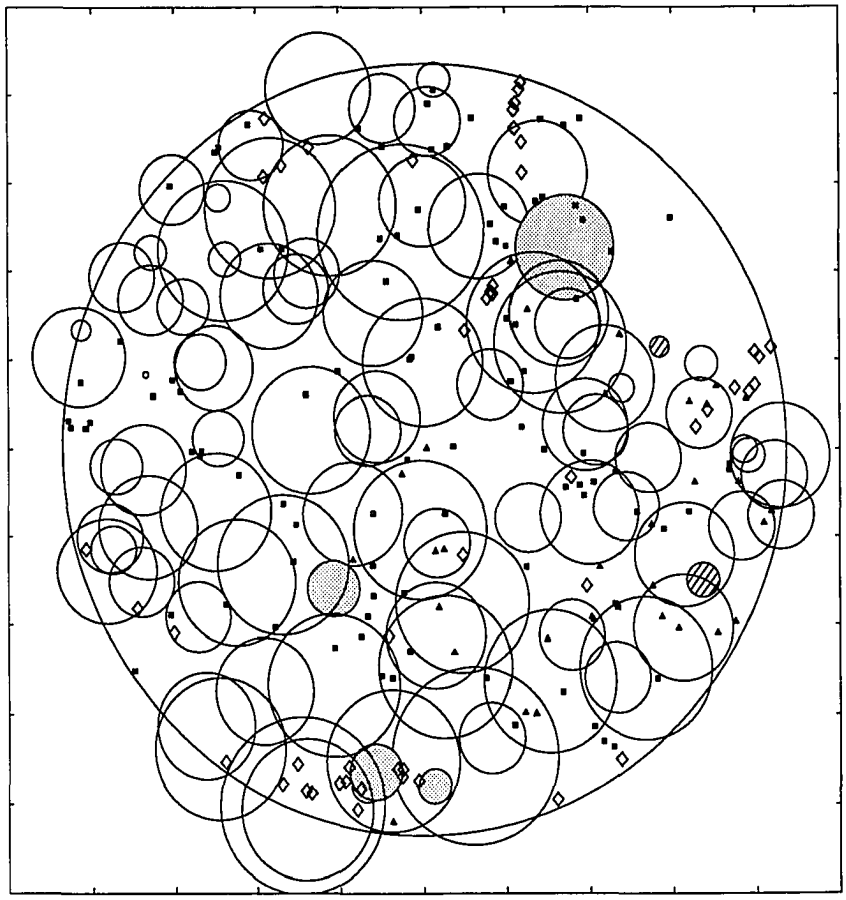


FIG. 22. Crown map for Stand 5 in the **BEPA-POTR/VIED c.t.**, indicating spatial arrangement of stems by species. Fill patterns are: ○ = *Betula papyrifera*, ▪ = seedling; ⊘ = *Populus tremuloides*, ▲ = sucker; ⊙ = *Picea glauca*, ◇ = seedling. Interval of grid is 2.5 meters.

($g' = 0.13$, $p < 0.1$). Both *B. papyrifera* and *P. glauca* occurred throughout as seedlings and sapling. *P. glauca* tended to be clustered together either directly under a *B. papyrifera* canopy or within a canopy gap, presumably in response to some microsite influence. Overstory canopy cover was estimated at 70 percent.

Stand 29 was dominated by *P. tremuloides*, and also contained *B. papyrifera, P. balsamifera* and *P. glauca* (Fig. 23). This stand contained 2,240 living stems; almost all of these stems were trees greater than 1.37 m in height. Crowns were large and overlapping, creating about 80 percent canopy cover. Mean crown diameter of *P. tremuloides* was 3.3 m. Crown diameters followed a bell-shaped frequency distribution ($g' = 0.27$, $p < 0.01$). Several *P. tremuloides* and *P. glauca* crowns exceeded 6 m in diameter.

A third canopy type is represented by Stand 30, which was composed primarily of large, open-spaced *B. papyrifera* (Fig. 24). Canopy cover of *B. papyrifera* was estimated at 60 percent in the field. Individual crowns ranged from 1.0 to 6.0 m in diameter. Several *Picea mariana* were clumped together, a result of layering. Not portrayed in Fig. 24 are dead *B. papyrifera*; there were about 270 per hectare with diameters ranging between 10 and 25 cm. Canopy cover of the dominant shrubs *Rosa acicularis* and *Viburnum edule* together account for more than 50 percent ground cover in this stand.

A tall shrub stratum in the **BEPA-POTR/VIED c.t.** includes *R. acicularis*,

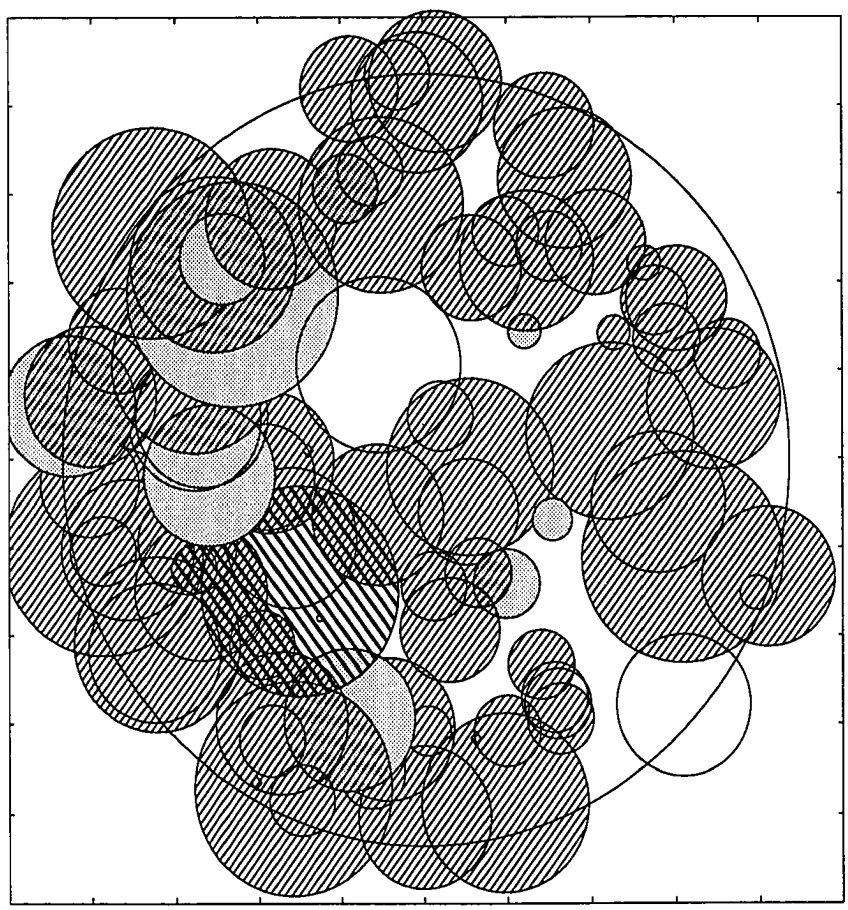


FIG. 23. Crown map for Stand 29 in the **BEPA-POTR/VIED c.t.**, indicating spatial arrangement of stems by species. Fill patterns are: ○ = *Betula papyrifera*; ⊘ = *Populus tremuloides*; ⊙ = *Picea glauca*, ◇ = seedling; ⊗ = *Populus balsamifera*. Interval of grid is 2.5 meters.

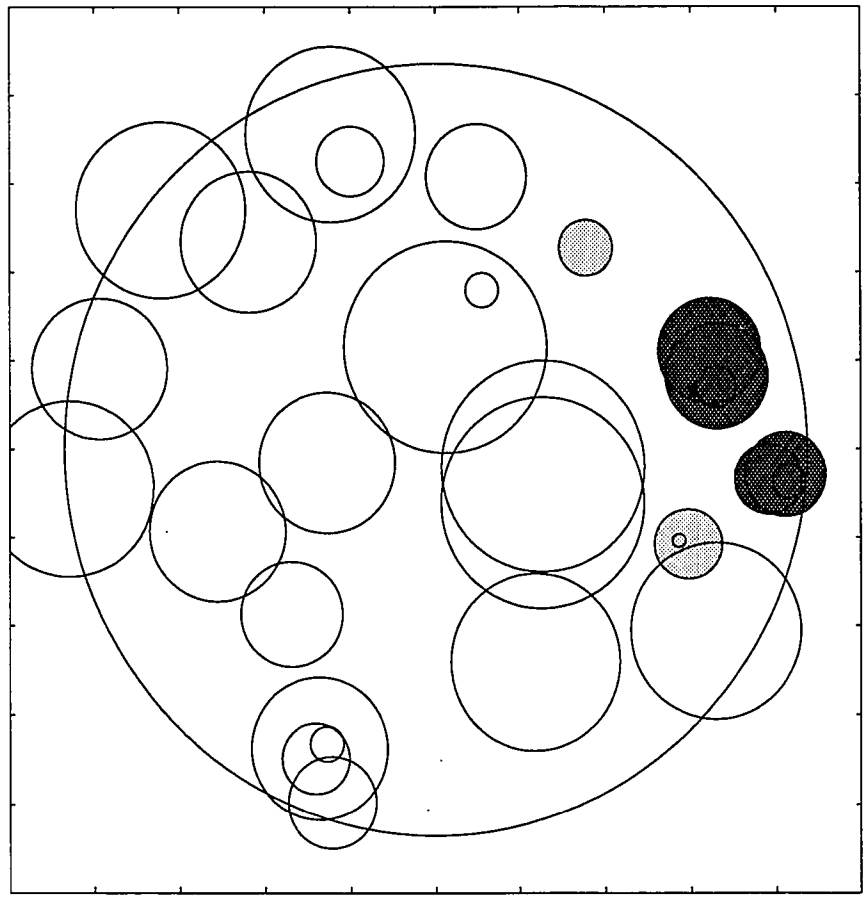


FIG. 24. Crown map for Stand 30 in the **BEPA-POTR/VIED c.t.**, indicating spatial arrangement of stems by species. Fill patterns are: ○ = *Betula papyrifera*; ⊙ = *Picea glauca*; ⊗ = *Picea mariana*. Interval of grid is 2.5 meters.

V. edule and sometimes *Alnus crispa*. Low shrubs include *Linnaea borealis* and sometimes *Vaccinium vitis-idaea*. When present, these low shrubs usually account for high ground cover. Cover of herbs is typically sparse. *Epilobium angustifolium, Cornus canadensis* and *Calamagrostis canadensis* have high constancy but usually low cover. *Equisetum arvense, Hylocomium splendens* and *Lycopodlum* species may occasionally have high ground cover.

Stand development and productivity -- Total age was determined for 45 *P. glauca*, 21 *B. papyrifera* and 17 *P. tremuloides*. The chronosequence of sampled stands in the **BEPA-POTR/VIED c.t.** ranges from 46 to 136 total years of age (Table 5). Most stands belong to the stem exclusion development stage because of high density of both living and dead stems in the small diameter classes. Mortality resulting from competition averages 1,520 stems per hectare and occurs in *B. papyrifera* and *P. tremuloides* stems. Late stem exclusion is marked by large mean diameters of both living and dead stems, with mortality averaging 178 stems per hectare. One stand belonging to the reinitiation development stage was sampled; the frequency distribution of stems by diameter classes was not normal or skewed, but instead different species had different bimodal distributions indicating an influx or reinitiation of stems in the undergrowth.

Two patterns of stand development occur within the **BEPA-POTR/VIED c.t.**, based on reconstruction of 81 trees. The dominant pattern of development is

Table 5. Age of overstory, sample size (N) and developmental characteristics of sample stands by chronosequence in the **BEPA-POTR/VIED c.t.**

Stand	Overstory			Development stage	Additional stems	
	Species[1]	Age	N		Species	Age
42	Bepa	46	1	Stem exclusion	Pigl	45
					Pigl	44
					Pigl	44
					Pigl	44
55	Bepa	53	2	Stem exclusion	Pigl	60
					Pigl	57
20	Potr	52 - 54	3	Stem exclusion	Bepa	55
					Bepa	53
					Pigl	53
					Pigl	49
					Pigl	48
6	Bepa	56	1	Stem exclusion	Pigl	66
					Pigl	61
					Pigl	61
					Pigl	59
					Pigl	59
					Pigl	55
5	Bepa	58 - 63	2	Stem exclusion	Pigl	55
29	Potr	62 - 63	3	Stem exclusion	Bepa	63
					Pigl	70
					Pigl	63
37	Bepa	64	3	Reinitiation	Potr	63
					Potr	60
					Pigl	69
					Pigl	63

(Cont.)

Stand	Overstory			Development stage	Additional stems	
	Species[1]	Age	N		Species	Age
50	Potr	65 - 66	2	Stem exclusion	Pigl	61
					Pigl	60
					Pigl	58
					Pigl	51
32	Potr	51 - 70	3	Stem exclusion	Pigl	51
					Pigl	50
					Pigl	47
					Pigl	43
39	Potr	56 - 72	2	Stem exclusion	Pigl	58
					Pigl	56
					Pigl	52
					Pigl	51
18	Potr	72 - 74	2	Stem exclusion	Pigl	75
					Pigl	74
16	Bepa	63 - 75	2	Late stem exclusion	Pigl	74
					Pigl	71
					Pigl	68
					Pigl	63
13	Bepa	62 - 82	3	Late stem exclusion	Pigl	76
					Pigl	76
					Pigl	75
					Pigl	74
30	Bepa	119 - 136	2	Late stem exclusion	Pigl	108
					Pigl	62
					Pigl	25

[1] Species codes are: Potr = *Populus tremuloides*, Pigl = *Picea glauca*, Bepa = *Betula papyrifera*

that of concurrent establishment of conifers and hardwoods within a relativeiy short period of time (Fig. 25 and 26), after which no additional regeneration occurs. There is no difference between mean number of years for estabiishment by species ($p > 0.66$, mean square error = 228.47 with 27 df). In many cases, these single-cohort stands contain *P. glauca* which precede the establishment of hardwoods by severai years. In other cases, hardwood species are the first on the site and are foilowed by *P. glauca* within severai years. Generally, sites are fuily occupied within 12 years foliowing a stand-replacing disturbance, and no additional establishment occurs until minor canopy disturbances lead to reinitiation of *P. tremuloides* suckering. With the exception of Stand 42 in which density of *P. glauca* exceeded 1,600 stems per hectare, other sampled stands in the c.t. contained iess than 250 *P. glauca* stems per hectare. Rate of *P. glauca* recruitment, based on maximum age of hardwoods in the overstory and observed mortality, is 64 stems per hectare per year over the 12-year period of recruitment.

In contrast to this dominant pattern of singie-cohort, rapid concurrent establishment, a second pattern of single-cohort but prolonged establishment was noted in stands 32, 39 and 30 (Fig. 27). This pattern is similar to that of the **POTR/ARUV** and **POTR/SHCA c.t.s** in that the hardwood component of these stands consists primarily of *P. tremuloides* which typically regenerates rapidly following a disturbance. *P. glauca* gradualiy filis in over a period of

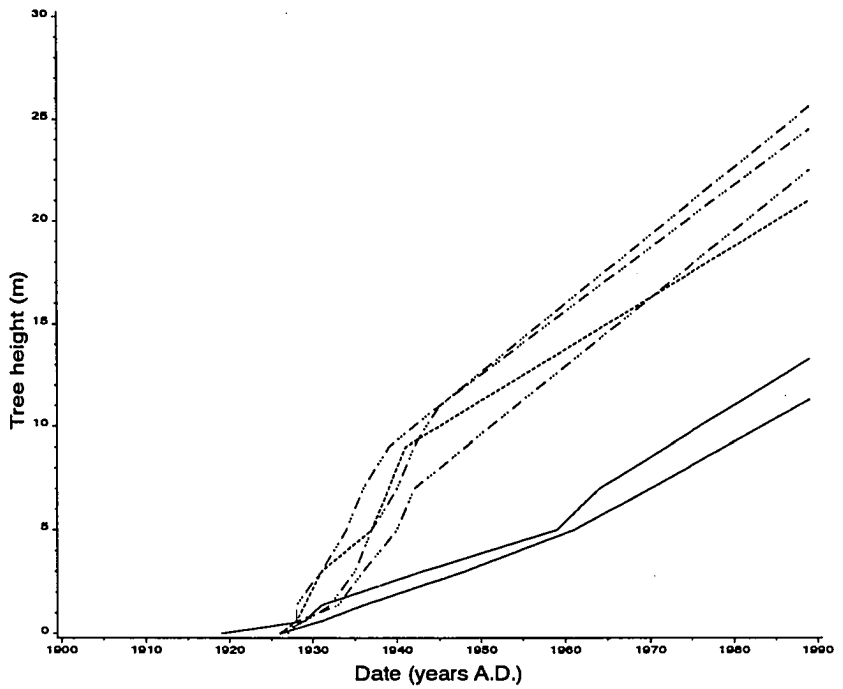


FIG. 25. Development of Stand 29 as a single-cohort, mixed species stand with a short establishment period. Legend for species composition is: *Populus tremuloides* = ··· — ··· - ; *Betula papyrifera* = --------- ; *Picea glauca* = ——— .

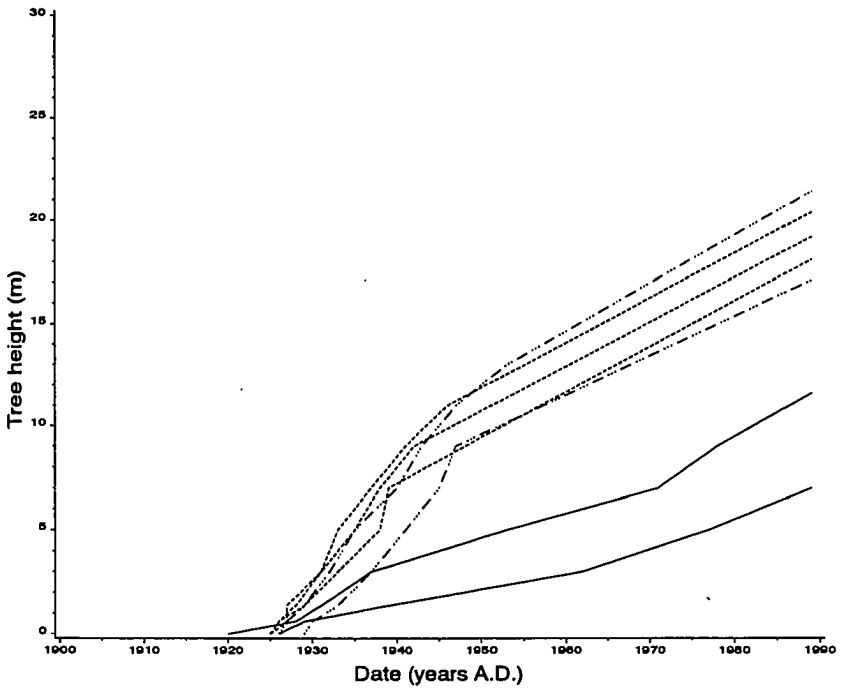


FIG. 26. Development of Stand 37 as a single-cohort, mixed species stand with a short establishment period. Legend for species composition is: *Populus tremuloides* = ··· — ··· - ; *Betula papyrifera* = --------; *Picea glauca* = ——— .

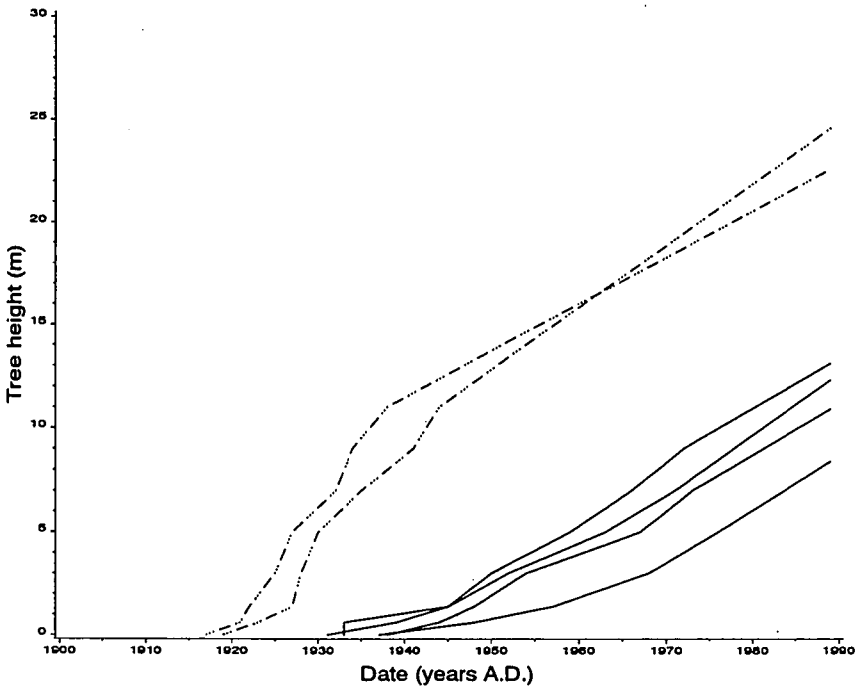


FIG. 27. Development of Stand 39 as a single-cohort, mixed species stand with a prolonged establishment period. Legend for species composition is: *Populus tremuloides* = ··· — ··· - ; *Picea glauca* = ——— .

several decades. Rate of *P. glauca* recruitment for this pattern of prolonged establishment, based on maximum age of the overstory and observed mortality, is 13 stems per hectare per year over three decades.

Evidence of past fire is common in these stands and may include charcoal, remnant stumps and even occasional snags and downed charred logs.

Vertical stratification is poorly expressed within hardwoods in the **BEPA-POTR/VIED c.t.** As with other *P. tremuloides*-dominated c.t.s previously described in this study, most *P. tremuloides* stems within a stand either maintain a position in the upper continuous canopy or are lost to mortality. *B. papyrifera* is also relatively intolerant of shade and, if present in the stand, must also maintain a position in the upper continuous canopy or be out-competed and die. When *B. papyrifera* and *P. tremuloides* occur together interspecific competition results in little difference in height growth patterns (Fig. 25 and 26).

Crown size directly influences diameter growth of stems and thus the horizontal stratification by diameter classes. Little difference in total height existed between the two *P. tremuloides* and three *B. papyrifera* in Stand 37 (Fig. 26). There was a 13 percent difference between the shortest and tallest *B. papyrifera* sampled for stem analysis; these same trees differ by more than 95 percent in diameter at breast height. Two *P. tremuloides* differ in total height by 25 percent and in diameter by 62 percent. Suppression in both *P. tremuloides* and *B. papyrifera* is evident in radial growth patterns (Fig. 28).

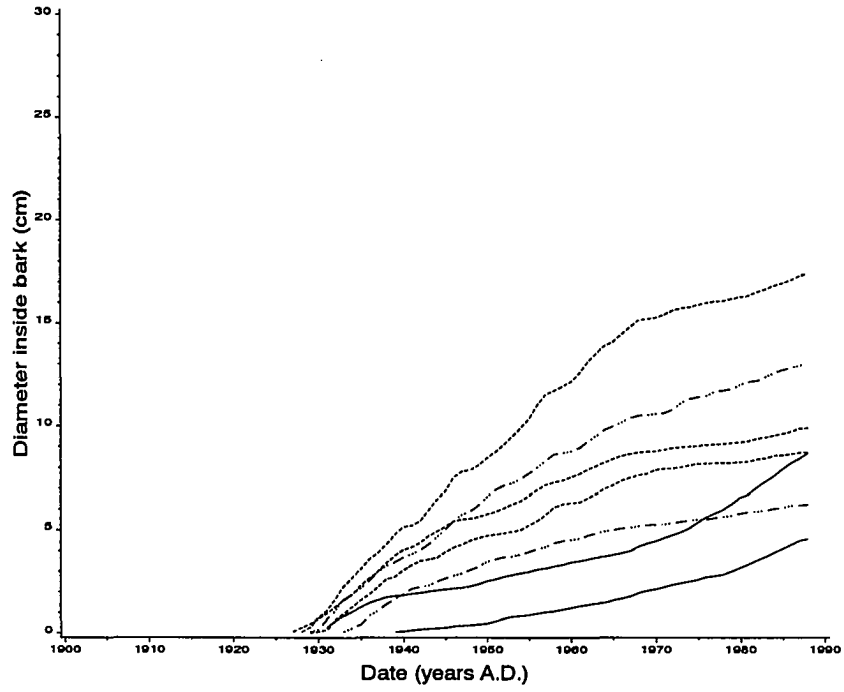


FIG. 28. Cumulative inside bark diameter growth patterns at breast height of representative trees in Stand 37. Legend for species composition is: *Populus tremuloides* = ··· — ··· - ; *Picea glauca* = ——— ; *Betula papyrifera* = --------- .

Height and diameter growth patterns for *P. glauca* in the **BEPA-POTR/VIED c.t.** indicate a strong relationship between growth and canopy position. Perhaps the most striking example is that of two *P. glauca* in Stand 55 (Fig. 29). About 60 years prior to sampling, conifers became established over several year; *B. papyrifera* followed several years later. One *P. glauca* maintained height growth consistent with that of the *B. papyrifera* while the other was rapidly overtopped. Diameter growth patterns for these same trees indicate the effect of suppression on the *P. glauca* growing under the *B. papyrifera* canopy compared to the consistent high rate of radial growth of the open-grown *P. glauca* (Fig. 30). Similar patterns of slow radial growth in *P. glauca* occurs in stands which have developed with a prolonged establishment period.

Additional changes which might occur within stands in this c.t. are difficult to predict. *B. papyrifera* in this portion of its range often develops stem decay with advancing age. Although usually short-lived, it sometimes persists for 150 to 200 years in the absence of fire. During this time, it may continue to exert a competitive influence on *P. glauca* in subordinate canopy positions. As *P. glauca* grows slowly through and above the *B. papyrifera* canopy, both radial and height growth of *P. glauca* may increase and *B. papyrifera* may be overtopped. Without additional recruitment of conifers, for which there is no evidence, these stands currently contain the maximum density of *P. glauca*

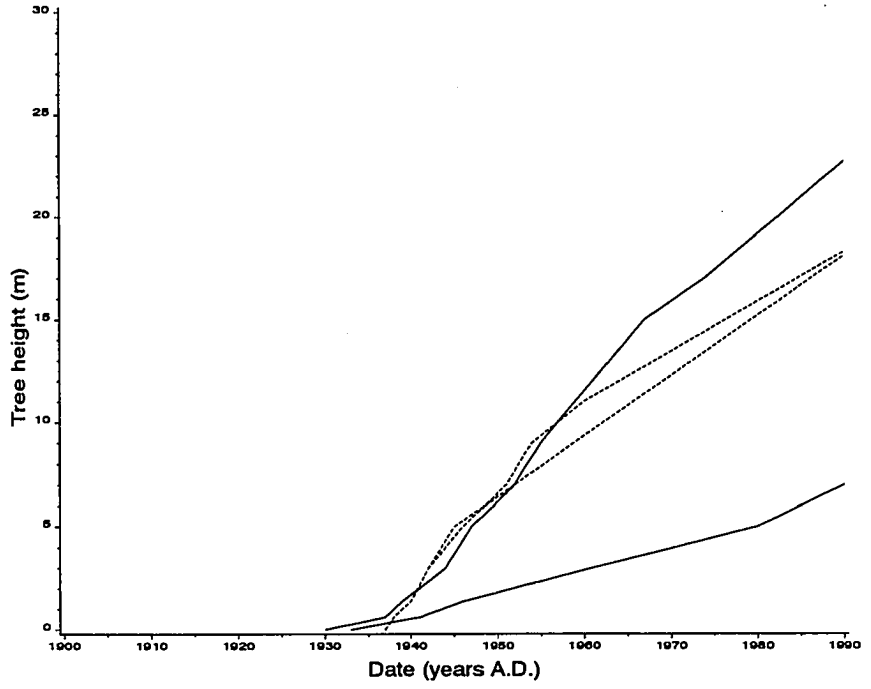


FIG. 29. Development of Stand 55 as a single-cohort, mixed species stand with a short establishment period. Legend for species composition is: *Betula papyrifera* = --------; *Picea glauca* = ———.

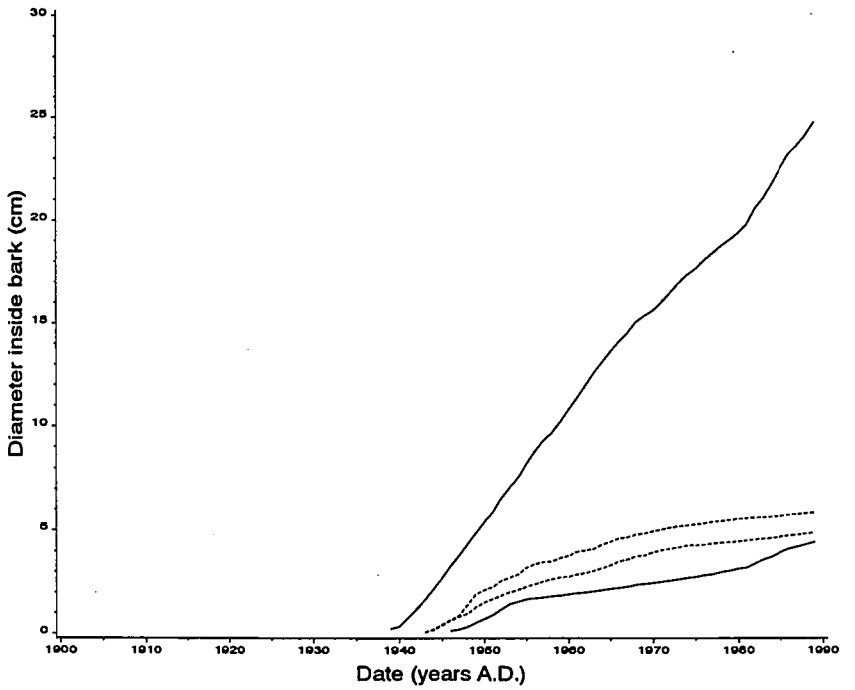


FIG. 30. Cumulative inside bark diameter growth patterns at breast height of representative trees in Stand 55. Legend for species composition is: *Picea glauca* = ——— ; *Betula papyrifera* = ---------.

potentially present in future stands. Assuming no additional mortality, density may vary between 50 and almost 2,000 *Picea glauca* stems per hectare. This c.t. is related to the **Picea glauca/Viburnum edule/Equisetum arvense/Hylocomium splendens c.t.** described by Foote (1983). Her type, described from two stands, is characterized by a closed canopy of *P. glauca* that may have developed from *P. tremuloides* and *B. papyrifera* stands. The undergrowth contains *V. edule, E. arvense* and *H. splendens.* Because these two stands are between 150 and 200 years in age, future stand dynamics are unclear.

Fifteen *P. glauca* sampled for stem analysis were open-grown and free of competition in the **BEPA-POTR/VIED c.t.**, and were used to construct a model depicting mean height growth (Table 6 and Fig. 31). A second group of 27 *P. glauca* with ring patterns indicating at least partial suppression was used to model the height growth of stand-grown or suppressed trees. *P. glauca* growing free of competition in this c.t. reach breast height in nine years, while *P. glauca* experiencing competition may require 15 years to reach the same height. After 50 years, open-growing *P. glauca* are slightly less than 15 m in height, and suppressed *P. glauca* are slightly more than 7 m. Both *P. tremuloides* and *B. papyrifera* have faster rates of growth initially and will overtop conifers for the first 50 years. *P. tremuloides* and *B. papyrifera* reach breast height in four years and are more than 15 m in height after 50 years.

Table 6. Species, number of sample trees, model parameters and error terms used in nonlinear regression models of height growth in the **BEPA-POTR/VIED c.t.**

Species[1]	N[2]	Model[3]	DF[4]	MSR	MSE	Estimated Parameters		ASE[5]
Open Pigl	15	CR	138	3709.00	3.52	θ_1 =	91.9430	99.618
						θ_2 =	0.0068	0.007
						θ_3 =	1.4758	0.239
Supp Pigl	27	CR	183	1904.66	4.22	θ_1 =	105.5591	236.188
						θ_2 =	0.0035	0.007
						θ_3 =	1.4639	0.304
Potr	14	NE	105	3495.73	5.76	θ_1 =	27.9909	3.764
						θ_2 =	0.0166	0.003
Bepa	12	NE	81	2444.45	1.97	θ_1 =	25.9433	1.856
						θ_2 =	0.0175	0.002

[1] Species codes are: Open Pigl = Open-grown *Picea glauca*; Supp Pigl = Suppressed *Picea glauca*; Potr = *Populus tremuloides*; Bepa = *Betula papyrifera*
[2] Number of trees in sample
[3] CR = Chapman-Richards; NE = Negative Exponential
[4] Uncorrected total degrees of freedom
[5] Asymptotic standard error

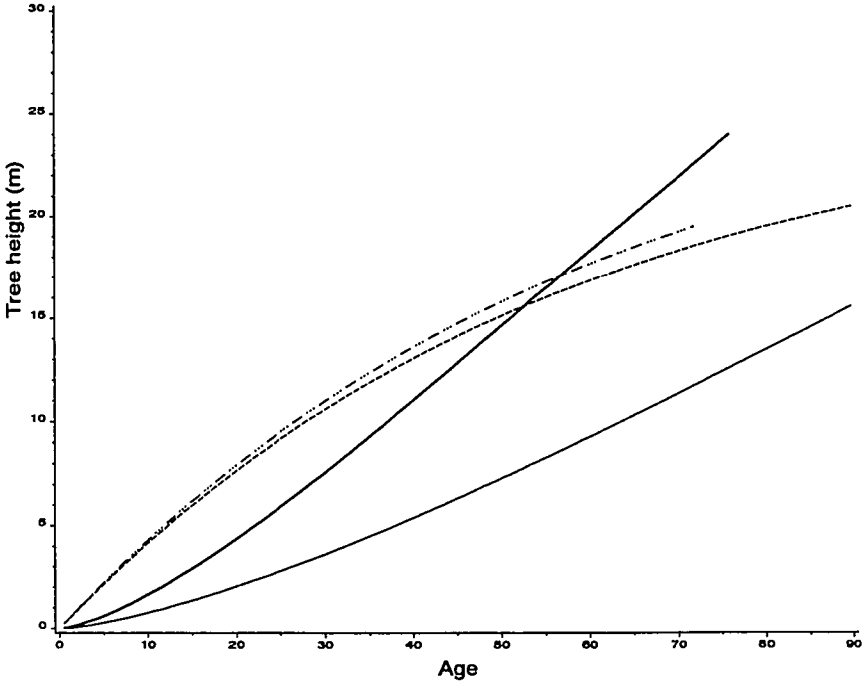
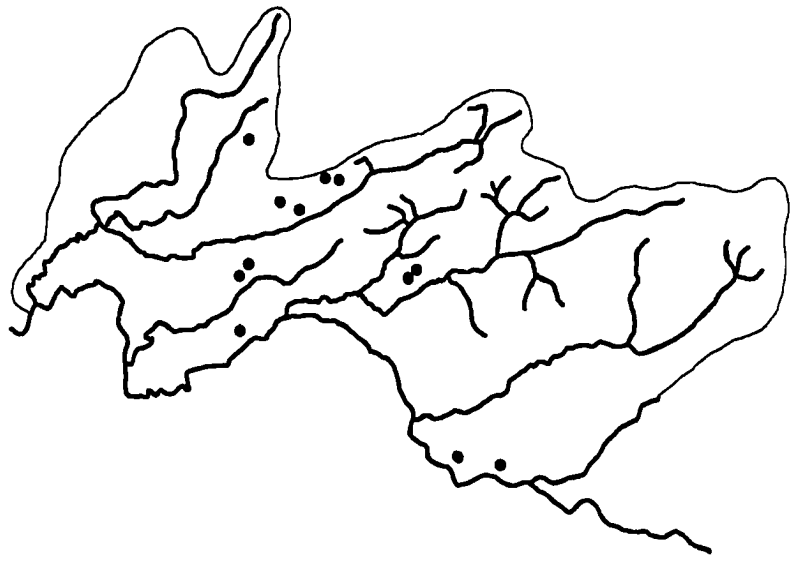


FIG. 31. Mean height growth in the **BEPA-POTR/VIED c.t.** Legend for species composition is: *Populus tremuloides* = ··· — ··· - ; *Betula papyrifera* = -------- ; Open-grown *Picea glauca* = ——— ; Suppressed *Picea glauca* = ——— .

Other studies -- Foote (1983) described two communities dominated by *B. papyrifera* and *V. edule* and three communities dominated by *P. tremuloides* and *V. edule* that may belong to this c.t. Her stands contain high canopy cover of *C. canadensis* and *E. arvense*, however, and exceed the stand age criterion of this study. The **BEPA-POTR/VIED c.t.** as described here represents a new Level V type in the Closed Paper Birch-Quaking Aspen Forest (I.B.1.f.) of Viereck *et al.* (in prep.).

Betula papyrifera-Populus tremuloides/Alnus crispa c.t.

BEPA-POTR/ALCR c.t.



Distribution -- The **BEPA-POTR/ALCR c.t.** is a major c.t. sampled throughout the study area between 240 and 580 m in elevation (mean = 360 m). It occurs on a variety of aspects but is most common on slopes with southeastern or southwestern exposure. The Latitude of Equivalent Slope ranges from 50 to 63° (mean = 57°), similar to the **POTR/SHCA** and **BEPA-POTR/VIED c.t.s.**

Common sites include mid and upper slopes with gentle to very steep gradients (mean = 21 percent) and straight configurations. Adjacent communities are often dominated by *Picea glauca* and *P. mariana*.

The **BEPA-POTR/ALCR c.t.** occurs on a wide variety of soils. Thick soils, in which depth to bedrock exceeds 1.0 m, are classified as Alfic Cryochrepts and are similar to those supporting the **BEPA-POTR/VIED c.t.** Most other soils are less developed and shallower and are classified as either Typic or Lithic Cryochrepts. Bedrock is within 0.8 m in Typic Cryochrepts and within 0.5 m in Lithic Cryochrepts. Surface organic accumulations within the c.t. are between 5 and 10 cm thick.

Vegetation composition and structure -- The **BEPA-POTR/ALCR c.t.** has the greatest diversity in species composition among the five c.t.s described in this study. Individual communities, however, are often simplistic in composition, with most of the cover consisting of a few species. The upper continuous canopy is usually dominated by *Betula papyrifera*. Grouped in this c.t., however, are additional stands in which *Populus tremuloides* dominates the overstory because of uniformity in undergrowth composition. Most communities contain *P. tremuloides* in both the upper or B-stratum and sometimes lower strata. Canopies range from 13 to 23 m in height when dominated by *B. papyrifera* and 14 to 19 m when dominated by *P. tremuloides*. *P. glauca* occurs in dominant, codominant, or intermediate canopy positions within the B-

stratum, a lower C-stratum, or as an individual emergent, extending several meters above the hardwood canopy. *P. mariana* may occur as individual stems or layered clumps. Density of living trees at least 1.37 m in height ranges from 960 to 4,100 stems per hectare (mean ± s.e. = 2,195 ± 313).

Frequency distribution of all stems by diameter class varies by species (Fig. 32). Total number of living stems ranges from 1,150 to over 10,200 per hectare (mean = 3,809 ± 780). *B. papyrifera* occurs with a bell-shaped distribution. Most *B. papyrifera* stems occur in the 5 to 15 cm diameter class. *P. tremuloides* occurs with a bimodal distribution; 760 suckers or small stems per hectare are less than 1.37 m in height, and about 380 stems per hectare are between 10 and 15 cm in diameter. *P. glauca* occurs most frequently as seedlings and *Picea mariana* as layerings; their distribution is heavily skewed to the right in a reverse "J" curve. Mortality is restricted to the smaller diameter classes of *B. papyrifera* and *P. tremuloides.*

Basal area per hectare in square meters of living trees at least 1.37 m in height (mean = 22.51 ± 1.55) and quadratic mean diameter in centimeters (mean = 12.29 ± 0.78) are similar to that in the **POTR/SHCA** and **BEPA-POTR/VIED c.t.s**. *B. papyrifera* accounts for 62 percent of the basal area and *P. tremuloides* accounts for 32 percent.

Stem maps from four sample stands portray the variability in spatial arrangement and crown structure of stems within the **BEPA-POTR/ALCR c.t.**

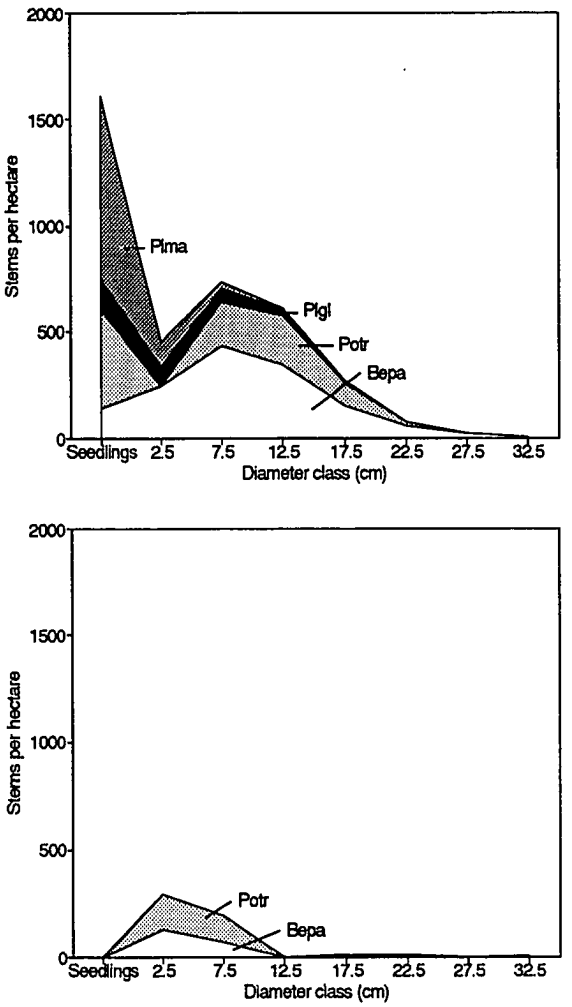


FIG. 32. Frequency distribution of living (above) and dead (below) stems by breast height diameter class and species in the **BEPA-POTR/ALCR c.t.**

Stand 3 was one of the most open stands, with total canopy cover estimated at 50 percent (Fig. 33); it contained 1,147 stems per hectare and 1,123 trees at least 1.37 m in height. Crowns of 25 *B. papyrifera* ranged from 1.2 to 4.8 m in diameter, with some clumping. Frequency distribution of B. papyrifera crown diameters was not skewed ($g' = 0.13$, $p < 0.01$). *P. mariana* tend to be aggregated together. Stand 2 contained 4,267 stems per hectare and 3,573 trees per hectare, and was dominated by *P. tremuloides* with crowns ranging from 0.4 to 6.8 m in diameter (Fig. 34). Trees were clustered together into dense clumps. Frequency distribution of 83 *P. tremuloides* crown diameters was skewed to the right ($g' = 1.17$, $p < 0.01$), with mean and median diameter approximately 2.0 m and crowns of 1.4 m in diameter occurring most frequently. *P. tremuloides* stems less than 1.37 m in height were notably absent. Like the previous stand, *P. mariana* was clustered, with many stems less than 1.37 m in height as a result of layering. *P. glauca* occurred only as well-established seedlings.

Stand 4 contained 2,747 living stems per hectare and 2,400 trees per hectare greater than 1.37 m in height (Fig. 35). Two-thirds of these were *P. tremuloides* distributed unequally within the stand. Fifty-nine *P. tremuloides* crowns ranged from 0.2 to 4.0 m in diameter in a bell-shaped distribution ($g' = 0.30$, $p < 0.01$) with mean diameter = 2.0 m. Scattered *B. papyrifera* ($n = 35$) within this stand had canopies ranging from 1.0 to 6.0 m in diameter

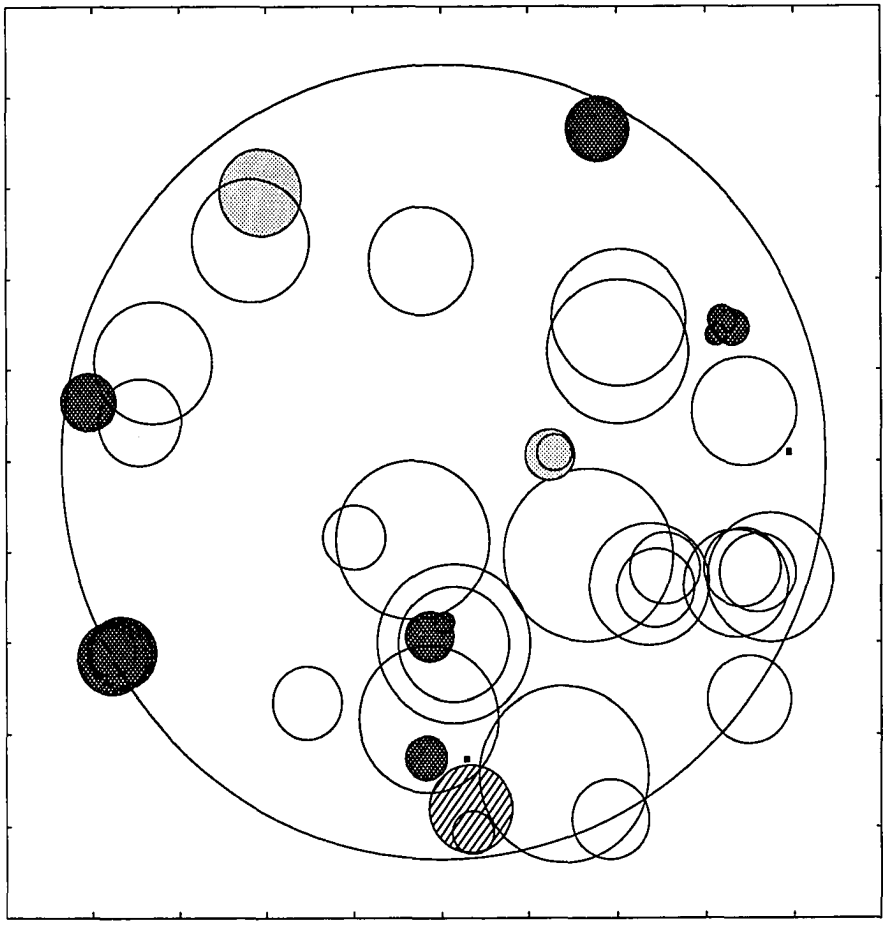


FIG. 33. Crown map for Stand 3 in the **BEPA-POTR/ALCR c.t.**, indicating spatial arrangement of stems by species. Fill patterns are: ○ = *Betula papyrifera*, ▪ = seedling; ⊘ = *Populus tremuloides*; ⊙ = *Picea glauca*; ⊗ = *Picea mariana*. Interval of grid is 2.5 meters.

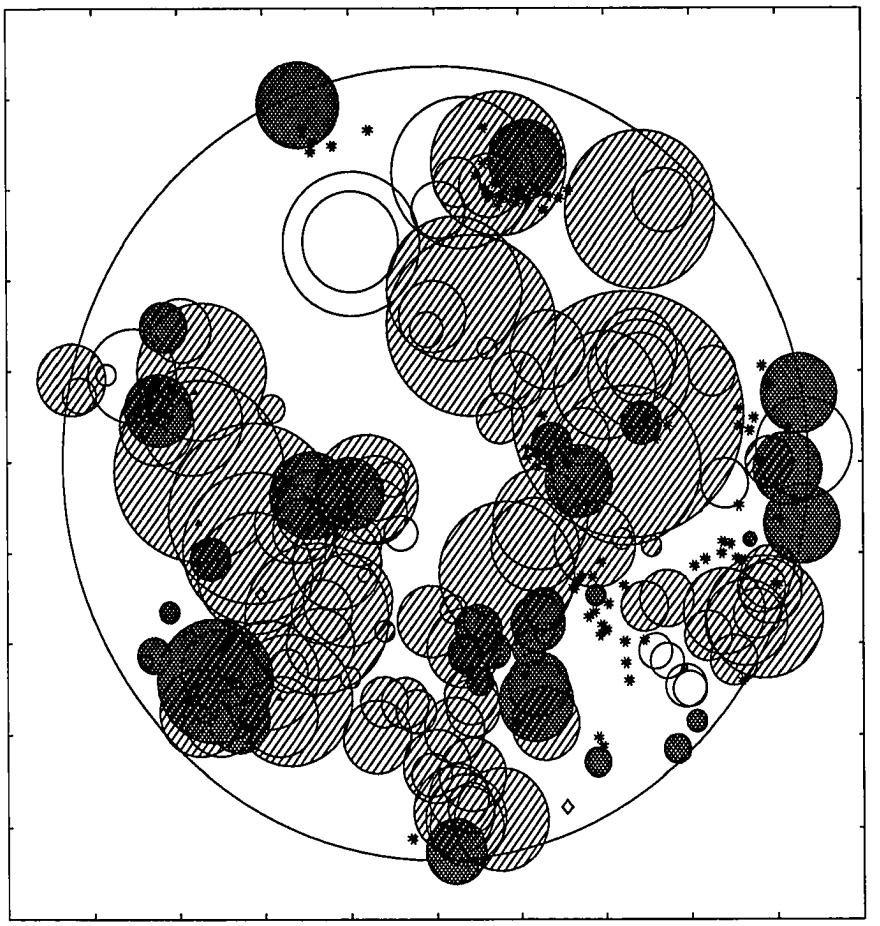


FIG. 34. Crown map for Stand 2 in the **BEPA-POTR/ALCR c.t.**, indicating spatial arrangement of stems by species. Fill patterns are: ○ = *Betula papyrifera*; ⊘ = *Populus tremuloides*, ▲ = sucker; ⊙ = *Picea glauca*, ◇ = seedling; ⊗ = *Picea mariana*, ✳ = seedling. Interval of grid is 2.5 meters.

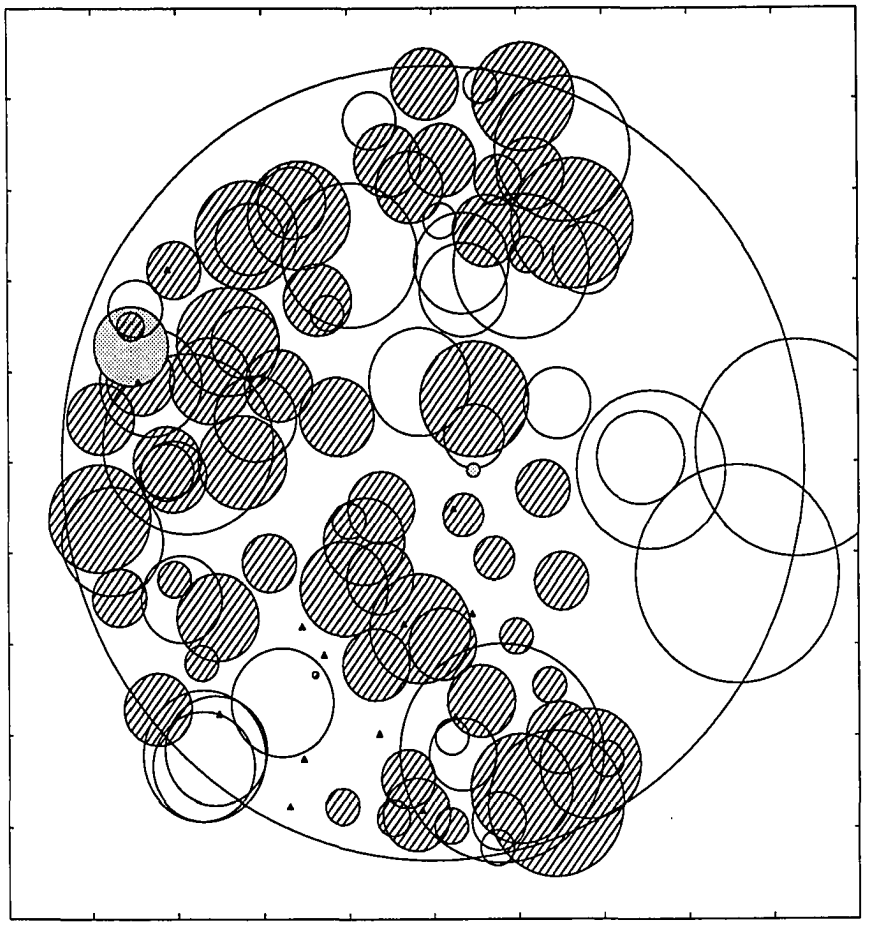


FIG. 35. Crown map for Stand 4 in the **BEPA-POTR/ALCR c.t.**, indicating spatial arrangement of stems by species. Fill patterns are: ○ = *Betula papyrifera*; ⊘ = *Populus tremuloides*, ▲ = sucker; ⊙ = *Picea glauca*. Interval of grid is 2.5 meters.

(mean = 2.6 m). Frequency distribution of these crown diameters was positively skewed ($g' = 0.94$, $p = 0.01$).

A final example of spatial arrangement is Stand 38, dominated by *B. papyrifera* (Fig. 36). This stand contained 2,480 living stems per hectare, and over 1,800 trees per hectare greater than 1.37 m in height. *B. papyrifera* crowns ranged from 0.2 to 6.2 m in diameter (mean = 2.0 m). Frequency of 60 *B. papyrifera* crown diameters followed a bell-shaped curve ($g' = -0.25$, $p < 0.01$). *P. glauca* stems were clustered in the upper portion of the sample plot. Crowns ranged from 0.2 to 2.0 m in diameter (mean = 0.9 m).

All four examples of stem mapping portray a common feature of stem and crown clustering, leaving canopy gaps over 25 to 50 percent of the forest floor. Regeneration, when present, was not restricted to these canopy gaps. Although field procedures did not specifically address gap characteristics, observations indicated that much of the apparent hole or gap in forest overstory was filled by tall shrubs in a lower stratum.

Alnus crispa is present as a distinctive, usually dense tall shrub stratum. In the most open stand which was stem mapped (Fig. 33), *A. crispa* occurred with 50 percent canopy cover. In Stands 2, 4 and 38 (Figs. 34, 35 and 36), canopy cover of *A. crispa* ranged from about 5 percent to 30 percent. Other shrubs that may occur with lesser canopy cover include *Rosa acicularis, Viburnum edule, Linnaea borealis* and *Vaccinium vitis-idaea*.

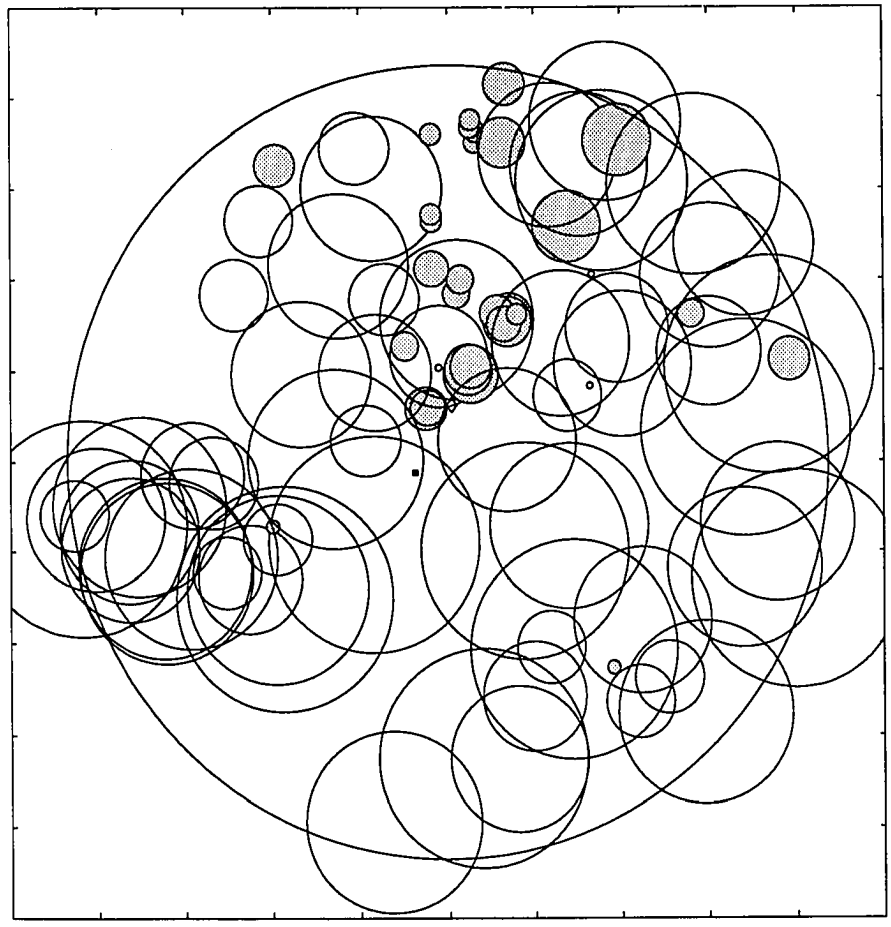


FIG. 36. Crown map for Stand 38 in the **BEPA-POTR/ALCR c.t.**, indicating spatial arrangement of stems by species. Fill patterns are: ○ = *Betula papyrifera*, ▪ = seedling; ⊙ = *Picea glauca*, ◇ = seedling. Interval of grid is 2.5 meters.

Numerous forbs and graminoids such as *Cornus canadensis, Epilobium angustifolium* and *Geocaulon lividum* may be present; none account for extensive ground cover. When present, cover of *Calamagrostis canadensis* may be abundant, and occurs within the same stands as the feathermoss *Hylocomium splendens. H. splendens* and the low shrub *Vaccinium vitis-idaea*, often are found growing on decaying downed logs in raised linear patches.

Stand development and productivity -- Total age wass determined for 30 *P. glauca*, 3 *P. mariana*, 30 *B. papyrifera* and 13 *P. tremuloides*. The chronosequence of sampled stands in the **BEPA-POTR/ALCR c.t.** includes a relatively narrow range extending from 59 to 71 total years of age, with one stand containing *Betula papyrifera* of 137 to 141 year old (Table 7). Most stands clearly belong to the stem exclusion development stage based on the number and diameter-class distribution of mortality. During the stem exclusion stage, competition between neighboring stems results in high mortality of stems with small diameters. Older stands belong to the stand reinitiation stage of development, during which advance regeneration becomes established in the undergrowth. Stands in the stand reinitiation stage contain more seedlings or suckers than small diameter stems and little mortality; dead stems are restricted to the larger diameter classes.

Two patterns of stand development occur within the **BEPA-POTR/ALCR c.t.** Many stands follow a pattern of rapid establishment, with hardwoods

Table 7. Age of overstory, sample size (N) and developmental characteristics of sample stands by chronosequence in the **BEPA-POTR/ALCR c.t.**

Stand	Overstory			Development stage	Additional stems	
	Species[1]	Age	N		Species	Age
3	Bepa	59	1	Stem exclusion	Potr	59
					Pigl	57
					Pigl	50
					Pima	60
					Pima	53
					Pima	45
2	Potr	60 - 61	2	Stem exclusion		
4	Potr	60 - 62	3	Stem exclusion	Bepa	59
					Bepa	49
					Pigl	56
27	Bepa	58 - 62	5	Stem exclusion	Pigl	58
					Pigl	57
28	Potr	54 - 63	3	Stem exclusion	Bepa	56
					Pigl	57
					Pigl	57
					Pigl	51
43	Bepa	51 - 63	2	Stem exclusion	Pigl	62
					Pigl	62
					Pigl	62
					Pigl	60
38	Bepa	62 - 63	5	Stem exclusion	Pigl	60
					Pigl	44
					Pigl	32
					Pigl	31

(Cont.)

Stand	Overstory			Development stage	Additional stems	
	Species[1]	Age	N		Species	Age
					Pigl	49
					Pigl	48
47	Bepa	63 - 65	2	Stem exclusion	Pigl	62
					Pigl	61
					Pigl	58
52	Potr	65	1	Reinitiation	Bepa	65
					Bepa	64
					Bepa	63
41	Potr	66 - 71	3	Stem exclusion	Bepa	61
					Pigl	59
					Pigl	59
33	Bepa	66 - 71	3	Stem exclusion	Pigl	63
					Pigl	60
31	Bepa	137 - 141	3	Reinitiation	Pigl	52
					Pigl	39
					Pigl	28
					Pigl	27
					Pigl	26

[1] Species codes are: Potr = *Populus tremuloides*, Pigl = *Picea glauca*, Bepa = *Betula papyrifera*, Pima = *Picea mariana*

regenerating within four years of a stand-replacing disturbance (Fig. 37 and 38). Establishment of *P. glauca* is concurrent with hardwoods ($p > 0.25$, mean square error = 445.06 with 26 df) establishment of conifers . Initial species composition and density is determined by propagule availabiiity within the short establishment window following disturbance, with little or no influx thereafter. When growing together, *P. tremuloides* and *B. papyrifera* often have similar height growth patterns. *P. glauca* is often subject to competition when growing through the hardwood canopy. Slow height growth may continue and often these trees show little promise of achieving dominance in the upper canopy.

In contrast, stands 38, 41 and 51 resulted from a different development pattern; rapid establishment of hardwoods was followed by establishment of conifers over a prolonged period of time lasting several decades (Fig. 39 and 40). Hardwood overstories include both *P. tremuloides* and *B. papyrifera*. No discernable difference in associated vegetation or site characteristics was detected between stands having this prolonged establishment of *P. glauca* and the more commonly encountered rapid establishment pattern.

Rate of *P. glauca* establishment, based on maximum age of hardwood species in each stand and observed mortality, is highly variable. Stands in which *P. glauca* becomes established concurrently with or shortly after hardwoods contain 230 *P. glauca* stems per hectare.

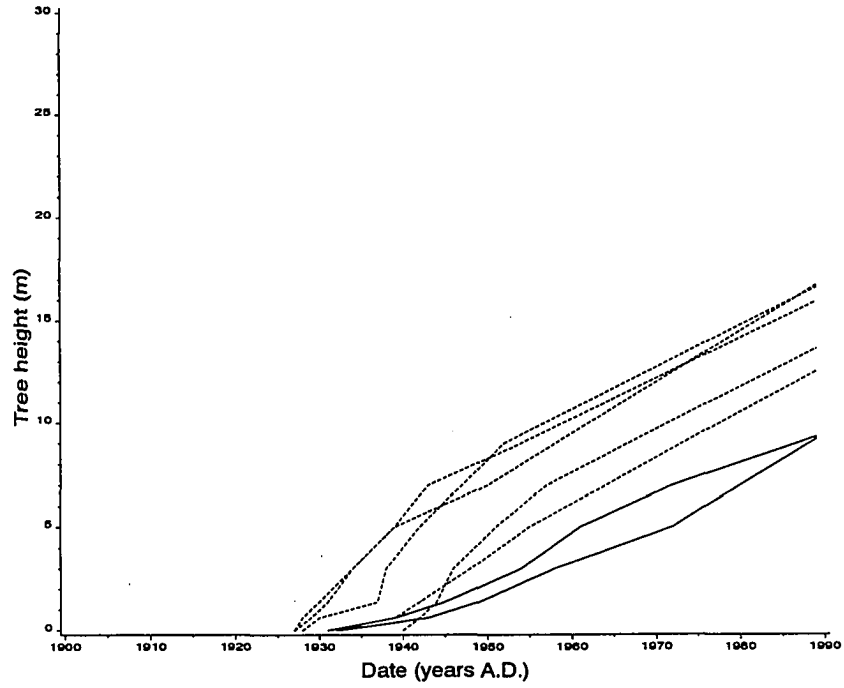


FIG. 37. Development of Stand 27 as a single-cohort, mixed species stand with a short establishment period. Legend for species composition is: *Betula papyrifera* = -------- ; *Picea glauca* = ——— .

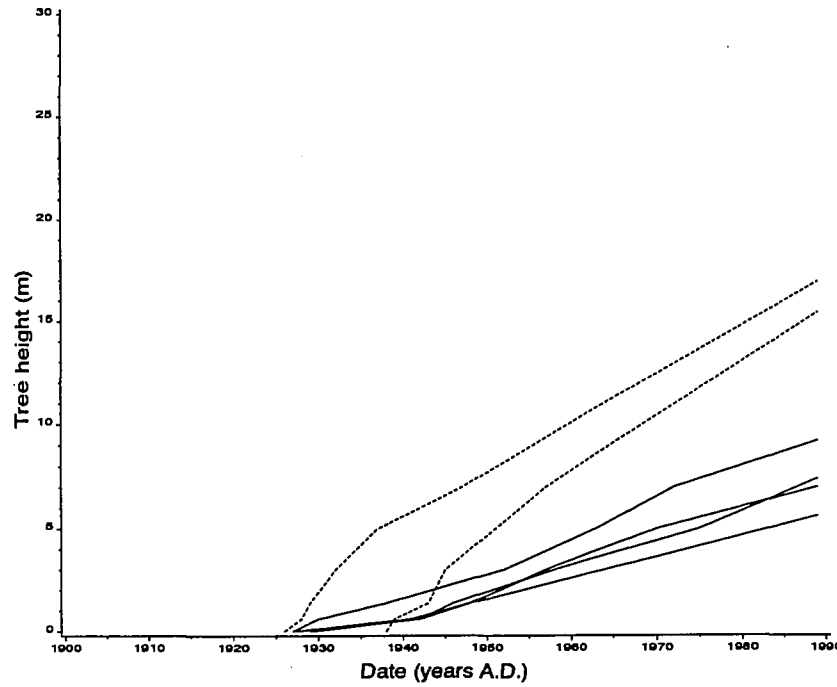


FIG. 38. Development of Stand 43 as a single-cohort, mixed species stand with a short establishment period. Legend for species composition is: *Betula papyrifera* = -------- ; *Picea glauca* = ——— .

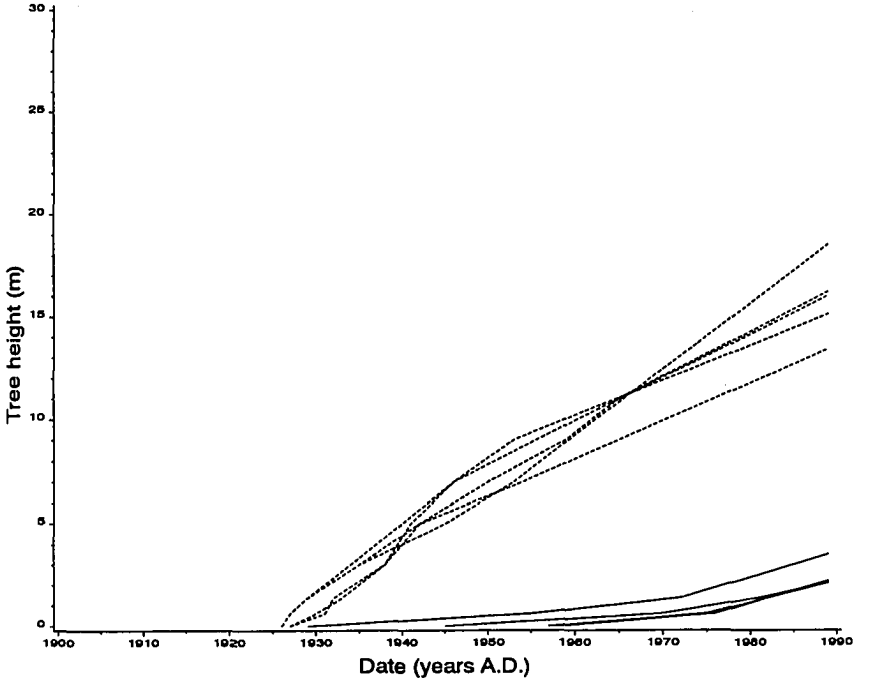


FIG. 39. Development of Stand 38 as a single-cohort, mixed species stand with a prolonged establishment period. Legend for species composition is: *Betula papyrifera* = -------- ; *Picea glauca* = ——— .

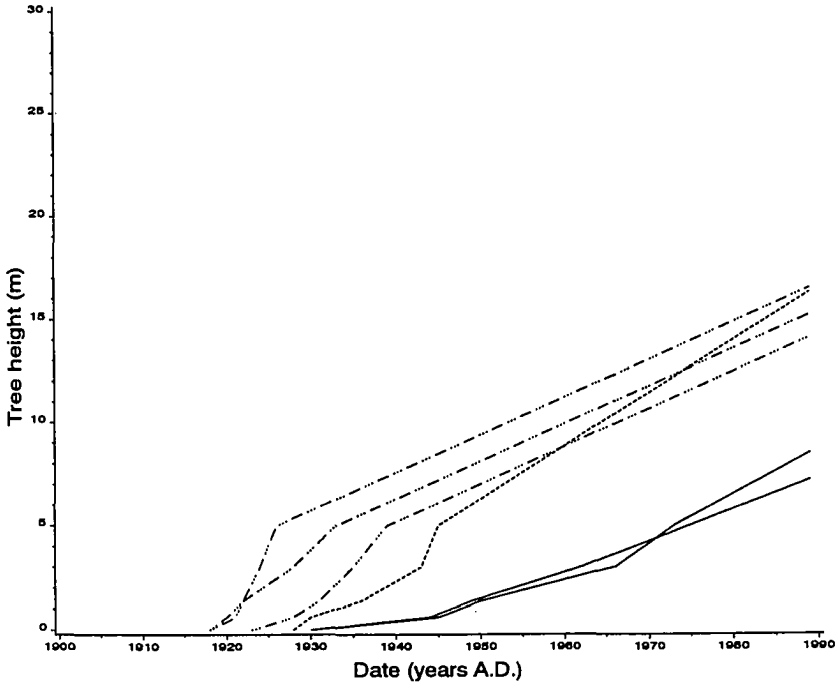


FIG. 40. Development of Stand 41 as a single-cohort, mixed species stand with a prolonged establishment period. Legend for species composition is: *Populus tremuloides* = ··· — ··· · ; *Betula papyrifera* = -------- ; *Picea glauca* = ——— .

Stem analysis data from eight *P. glauca* were used to model mean height growth of open-grown, competition-free trees in the **BEPA-POTR/ALCR c.t.** (Table 8 and Fig. 41). Many more stems had ring width families and ring area increments indicative of suppression. This second group of 27 *P. glauca* was used to model the height growth of suppressed trees. *P. glauca* growing free of competition in this c.t. reach a height of 1.37 m in nine years, while *P. glauca* experiencing competition require 18 years to reach the same height. After 50 years, open-growing *P. glauca* are almost 14 m in height, and suppressed *P. glauca* are 6 m tall. *P. tremuloides* and *B. papyrifera* have faster rates of initial growth. *P. tremuloides* are at least 1.37 m tall after five years and *B. papyrifera* are the same height after four years. Height growth has slowed in *P. tremuloides* by 50 years of age, when the top of the canopy is 15 m above the forest floor. Height growth of *B. papyrifera* is less than that of *P. tremuloides* but continues longer. At 50 years of age, *B. papyrifera* are almost 14 m tall and may surpass *P. tremuloides* after 65 years. Only in this **BEPA-POTR/ALCR c.t.** were *P. tremuloides* height growth data modelled better with the three parameter Chapman-Richards model rather than the negative exponential model.

Other studies -- Foote (1983) briefly described two communities belonging to a **Betula papyrifera/Alnus crispa/Calamagrostis canadensis c.t.** that may be related to this c.t. Her stands were aged at 50 and 130 years and apparently

Table 8. Species, number of sample trees, model parameters and error terms used in nonlinear regression models of height growth in the **BEPA-POTR/ALCR c.t.**

Species[1]	N[2]	Model[3]	DF[4]	MSR	MSE	Estimated Parameters		ASE[5]
Open Pigl	8	CR	60	927.47	1.79	θ_1 =	382.8290	3717.066
						θ_2 =	0.0016	0.013
						θ_3 =	1.3152	0.312
Supp Pigl	22	CR	128	612.75	2.07	θ_1 =	9.9040	2.563
						θ_2 =	0.0362	0.017
						θ_3 =	2.6519	1.015
Potr	12	CR	104	2369.81	1.67	θ_1 =	17.0191	0.640
						θ_2 =	0.0534	0.007
						θ_3 =	1.7559	0.210
Bepa	22	NE	166	4132.03	1.42	θ_1 =	24.1652	1.594
						θ_2 =	0.0168	0.002

[1] Species codes are: Open Pigl = Open-grown *Picea glauca*; Supp Pigl = Suppressed *Picea glauca*; Potr = *Populus tremuloides*
[2] Number of trees in sample
[3] CR = Chapman-Richards; NE = Negative Exponential
[4] Uncorrected total degrees of freedom
[5] Asymptotic standard error

lack the diversity in species represented by this **BEPA-POTR/ALCR c.t.** The **BEPA-POTR/ALCR c.t.** as described here represents a new Level V type in the Closed Paper Birch-Quaking Aspen Forest (I.B.1.f.) of Viereck *et al.* (in prep.).

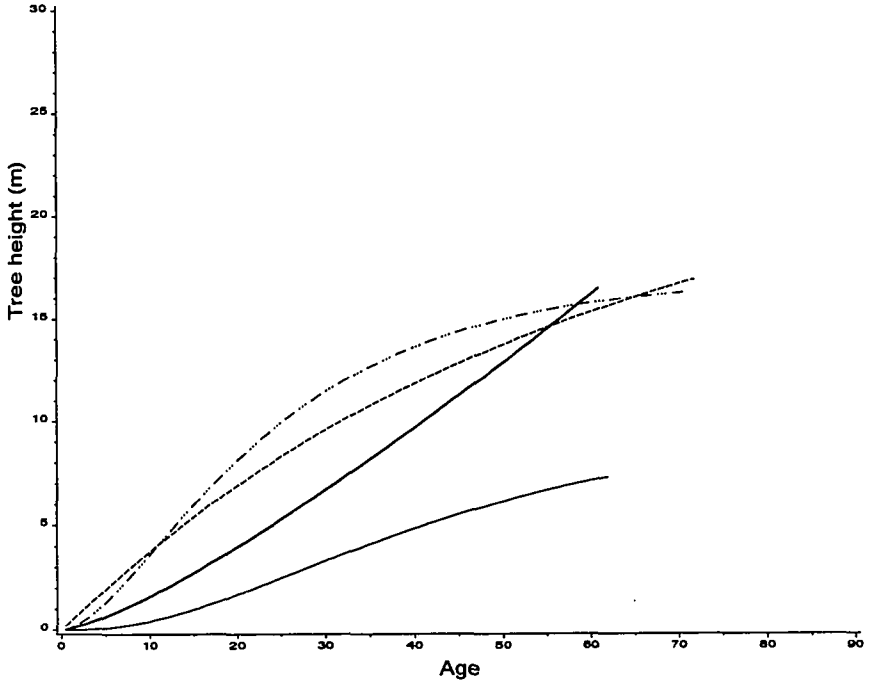
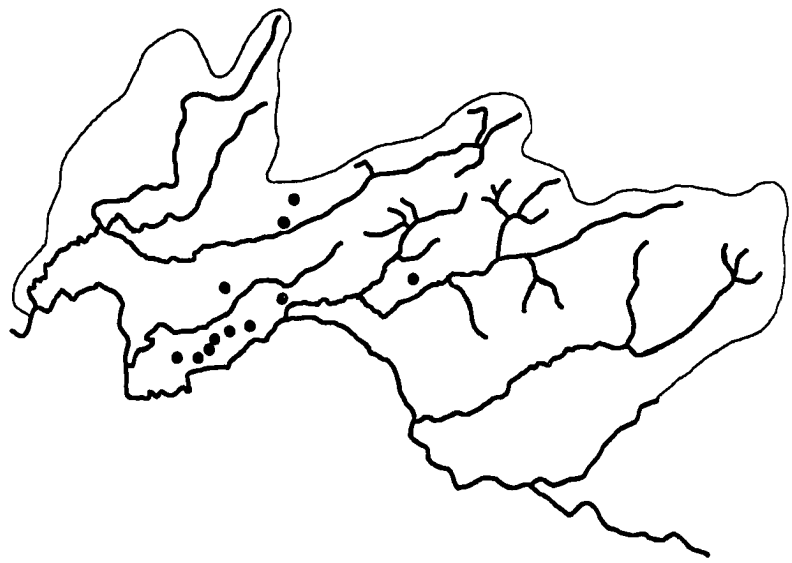


FIG. 41. Mean height growth in the **BEPA-POTR/ALCR c.t.** Legend for species composition is: *Populus tremuloides* = ··· — ··· - ; *Betula papyrifera* = -------- ; Open-grown *Picea glauca* = ——— ; Suppressed *Picea glauca* = ——— .

Picea glauca-Betula papyrifera/Hylocomium splendens c.t.

PIGL-BEPA/HYSP c.t.



Distribution -- The **PIGL-BEPA/HYSP c.t.** is a major c.t. sampled throughout the study area on eastern and southeastern slopes. It occurs most frequently on gentle to moderately steep mid and lower slopes with straight configuration and on mid slope benches. Elevations range from 150 to 430 m (mean = 260 m). The Latitude of Equivalent Slope ranges from 60 to 65° (mean = 63°).

A majority of the sampled communities belonging to the **PIGL-BEPA/HYSP c.t.** are underlaid with Alfic Cryochrepts that are coarse-silty and have mixed mineralogy. These soils have thin layers of accumulated silicate clays within the profile from weathering of the micaceous loess. High elevation sites may have shallow soils classified as Lithic Cryochrepts, which are more common in the **BEPA-POTR/ALCR c.t.** Occasionally, stands on the toe of slopes that have been influenced by changing drainage patterns have soils that contain permafrost and are classified as Aeric Cryaquepts. Depth of surface organic accumulations is highly variable within this c.t. and ranges from 5 to 15 cm.

Vegetation composition and structure -- The **PIGL-BEPA/HYSP c.t.** describes stands dominated by a mixture of *Picea glauca* and *Betula papyrifera*. Within the c.t., vertical stratification of canopies is readily apparent. *P. glauca* occurs as a dominant, codominant or intermediate in the upper continuous canopy or extends above the continuous canopy as an emergent with heights ranging from 10 to 21 m. *B. papyrifera* may occupy similar positions within the canopy, and ranges from 14 to 19 m in total height. *Populus tremuloides* occurs less frequently than does *P. glauca* or *B. papyrifera*, and is found in various canopy positions including emergent. Maximum heights of *P. tremuloides* range from 16 to 22 m. Both *Picea mariana* and *Populus balsamifera* occur occasionally; *P. mariana* is usually restricted to a lower C-stratum or an undergrowth layer and *P. balsamifera* is usually restricted to an

intermediate position in the B-stratum.

Density of all living trees at least 1.37 m in height ranges from 1,360 to 4,933 stems per hectare (mean ± s.e. = 2,759 ± 386), similar to the **BEPA-POTR/VIED c.t.** Compared to other c.t.s described in this study, relatively few stems less than 1.37 m in height are found in this c.t. Total number of living stems ranges from 1,573 to 5,813 (mean = 3,084 ± 415), a difference of 325 stems per hectare less than 1.37 m in height.

Living *P. glauca* stems occur in a bell-shaped skewed frequency distribution across diameter classes, with more than 50 percent of the stems between 5 and 15 cm in diameter at breast height (Fig. 42). Sixty percent of the *B. papyrifera* stems are less than 10 cm in diameter at breast height. Distribution of *P. tremuloides* stem is usually uniform across diameter classes. Mortality is most frequent in small diameter *P. glauca* and *B. papyrifera.*

Basal area per hectare in square meters ranges from 8.33 to 44.13 (mean = 29.86 ± 2.83). Quadratic mean diameter in centimeters ranges from 8.3 to 17.73 (mean = 12.44 ± 0.88). Both these measures of stem size for trees at least 1.37 m in height indicate diameters found in this c.t. are similar to those of the **POTR/SHCA, BEPA-POTR/VIED** and **BEPA-POTR/ALCR c.t.s.**

Stem maps are not available for representative stands within this c.t.

Cover of shrubs, forbs and graminoids is usually sparse. Occasionally,

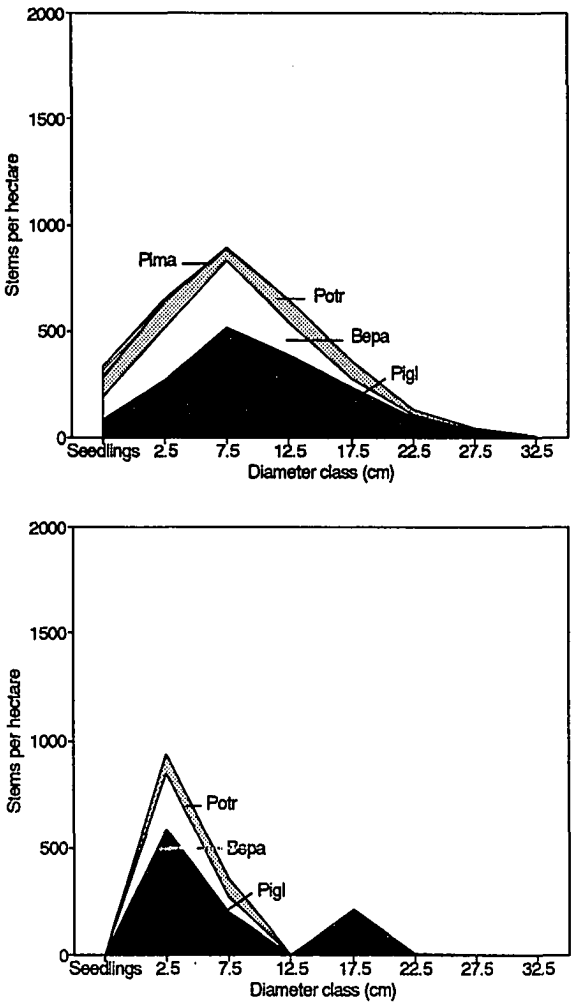


FIG. 42. Frequency distribution of living (above) and dead (below) stems by breast height diameter class and species in the **PIGL-BEPA/HYSP c.t.**

clumps of *Alnus crispa, Rosa acicularis, Viburnum edule, Vaccinium vitis-idaea* and *Linnaea borealis* may account for moderate amounts of ground cover. *Mertensia paniculata* is a common forb. *Calamagrostis canadensis* is notably absent. A dense, nearly complete cover of feathermosses is typical; sometimes this moss layer will be mixed with *Equisetum arvense.*

Stand development and productivity -- Total age was determined for 33 *P. glauca,* 1 *P. mariana,* 13 *B. papyrifera* and 7 *P. tremuloides.* The chronosequence of sampled stands in the **PIGL-BEPA/HYSP c.t.** extends from 57 to 107 total years of age (Table 9). All stands belong to the stem exclusion development stage based on the number of dead stems of small diameter. Mortality of small diameter *P. glauca* and *B. papyrifera* is common within this c.t., suggesting a continual reduction in density resulting from competition. The oldest stand sampled in this c.t. contained numerous *P. mariana* seedlings for which total age was not accurately determined. These seedlings may indicate a transition from the stem exclusion stage to the reinitiation stage, in which advance regeneration becomes established in the undergrowth.

Two patterns of stand development occur with this c.t. Most stands follow a pattern of rapid establishment of multiple species within a short period of time (Fig. 43 and 44). Hardwoods are usually the first to establish following a stand-replacing disturbance. Establishment of hardwoods is usually complete after six years. Establishment of conifers is concurrent; there is not difference between

Table 9. Age of overstory, sample size (N) and developmental characteristics of sample stands by chronosequence in the **PIGL-BEPA/HYSP c.t.**

Stand	Overstory			Development stage	Additional stems	
	Species[1]	Age	N		Species	Age
1	Bepa	57 - 58	3	Stem exclusion		
7	Pigl	61 - 63	3	Stem exclusion		
53	Bepa	52 - 64	2	Stem exclusion	Potr	63
					Potr	63
					Pigl	52
					Pigl	47
					Pigl	25
40	Bepa	64	1	Stem exclusion	Pigl	58
					Pigl	57
					Pigl	52
					Pigl	50
34	Potr	64 - 71	2	Stem exclusion	Bepa	64
					Bepa	64
					Bepa	64
					Bepa	63
					Bepa	61
					Pigl	63
					Pigl	62
					Pigl	62
					Pigl	62
					Pigl	60
					Pigl	60
46	Pigl	63 - 73	2	Stem exclusion	Bepa	75
22	Pigl	73	4	Stem exclusion		

(Cont.)

Stand	Overstory			Development stage	Additional stems	
	Species[1]	Age	N		Species	Age
17	Pigl	71 - 75	2	Stem exclusion	Bepa	74
15	Potr	74 - 75	2	Stem exclusion	Pigl	74
					Pigl	65
23	Pigl	74 - 76	4	Stem exclusion	Potr	85
54	Pigl	104 - 107	3	Stem exclusion	Pima	103

[1] Species codes are: Potr = *Populus tremuloides*, Pigl = *Picea glauca*, Bepa = *Betula papyrifera*, Pima = *Picea mariana*

mean number of years for establishment of the different species in this c.t. ($p < 0.64$, mean square error = 69.70 with 17 df). Occasionally *P. tremuloides* will continue to sucker 10 years after the stand-replacing disturbance. Rate of *P. glauca* recruitment for this c.t., based on overstory age and observed mortality, is 477 trees per hectare per year over a seven-year period. After the initial establishment period, few additional stems enter the stand.

An exception to the general pattern of rapid, concurrent establishment is evident in Stand 53. In this stand, initial hardwood establishment was followed by prolonged establishment of *P. glauca* (Fig. 45). Prolonged establishment of *P. glauca* occurs within *P. tremuloides*-dominated stands in the **POTR/ARUV** and **POTR/SHCA c.t.s** and occasionally within the **BEPA-POTR/VIED** and **BEPA-POTR/ALCR c.t.s** in both *B. papyrifera* and *P. tremuloides*-dominated stands.

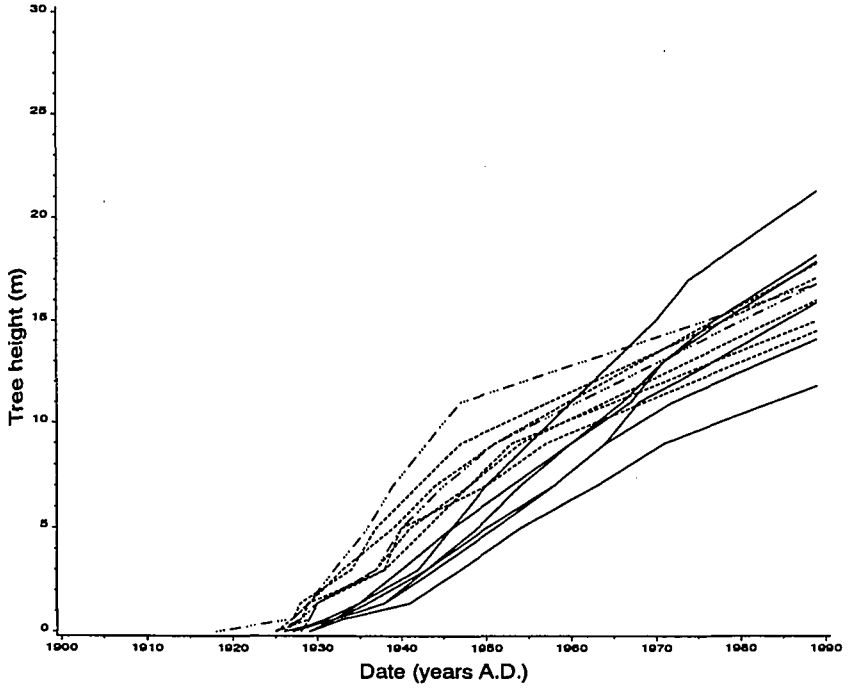


FIG. 43. Development of Stand 34 as a single-cohort, mixed species stand with a short establishment perlod. Legend for species composition is: *Populus tremuloides* = ··· — ··· - ; *Betula papyrifera* = -------- ; *Picea glauca* = ——— .

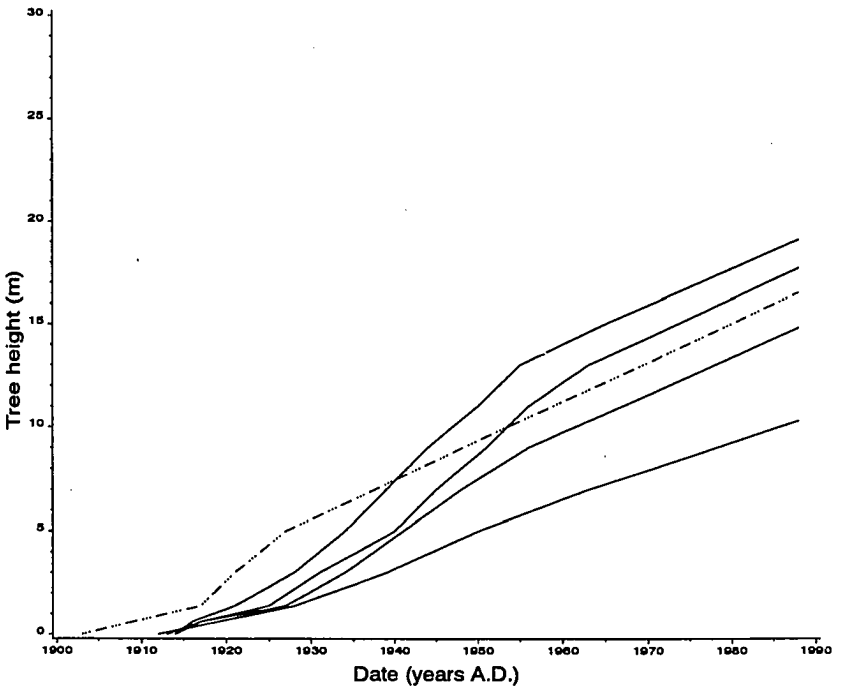


FIG. 44. Development of Stand 23 as a single-cohort, mixed species stand with a short establishment period. Legend for species composition is: *Populus tremuloides* = ··· — ··· - ; *Picea glauca* = ——— .

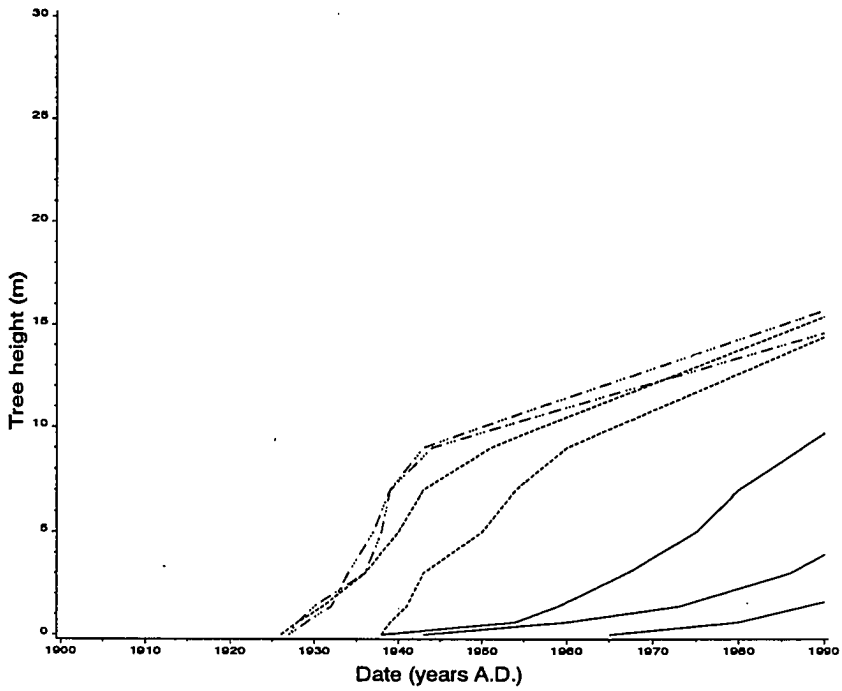


FIG. 45. Development of Stand 53 as a single-cohort, mixed species stand with a prolonged establishment period. Legend for species composition is: *Populus tremuloides* = ··· — ··· - ; *Betula papyrifera* = -------- ; *Picea glauca* = ——— .

Charcoal and charred downed logs are present in most stands. This suggests that the most common stand-replacing event is a fire.

Vertical stratification of species is poorly expressed in the **PIGL-BEPA/HYSP c.t.** because these single-cohort, mixed species stands are often dominated by *P. glauca* of uniform age.

Sixteen *P. glauca* sampled for stem analysis were open-grown and free of competition in the **PIGL-BEPA/HYSP c.t.**, and were used to construct a nonlinear model depicting mean height growth (Table 10 and Fig. 46). Seventeen additional trees were grouped to model the height growth of suppressed *P. glauca*. *P. glauca* growing free of competition in this c.t. reach a height of 1.37 m in slightly more than nine years, similar to that in the **BEPA-POTR/VIED** and **BEPA-POTR/ALCR c.t.s**. Suppressed *P. glauca* reach the same height in 14 years, similar to initial growth in the **BEPA-POTR/VIED c.t.** After 50 years, open-growing *P. glauca* are slightly less than 14 m in height, and suppressed *P. glauca* are almost 9 m. *P. tremuloides* and *B. papyrifera* have nearly identical height growth curves. Both species require four years to reach breast height and after 50 years are about the same height as *P. glauca*. Both hardwoods were fit with the negative exponential model.

Other studies -- This c.t. has not been previously described. Based on both overstory and undergrowth species composition and stem density, this c.t. is probably related to the *P. glauca*/feathermoss vegetation type (Viereck 1975).

Table 10. Species, number of sample trees, model parameters and error terms used in nonlinear regression models of height growth in the **PIGL-BEPA/HYSP c.t.**

Species[1]	N[2]	Model[3]	DF[4]	MSR	MSE	Estimated Parameters		ASE[5]
Open Pigl	16	CR	160	4116.59	3.39	θ_1 =	24.8263	3.408
						θ_2 =	0.0265	0.007
						θ_3 =	1.9240	0.306
Supp Pigl	17	CR	138	23.7.98	3.44	θ_1 =	24.4190	4.875
						θ_2 =	0.0178	0.006
						θ_3 =	1.8891	0.340
Potr	7	NE	45	1426.13	3.01	θ_1 =	28.8022	3.059
						θ_2 =	0.0132	0.003
Bepa	11	NE	79	2124.29	0.98	θ_1 =	27.3000	2.423
						θ_2 =	0.0141	0.002

[1] Species codes are: Open Pigl = Open-grown *Picea glauca*; Supp Pigl = Suppressed *Picea glauca*; Potr = *Populus tremuloides*; Bepa = *Betula papyrifera*
[2] Number of trees in sample
[3] CR = Chapman-Richards; NE = Negative Exponential
[4] Uncorrected total degrees of freedom
[5] Asymptotic standard error

His broadly-defined type includes floodplain sites, however, which are excluded from consideration in this study. The **PIGL-BEPA/HYSP c.t.** as described here represents a new Level V type in the Closed Spruce-Paper Birch-Quaking Aspen Forest (i.C.1.f.) of Viereck *et al.* (in prep.).

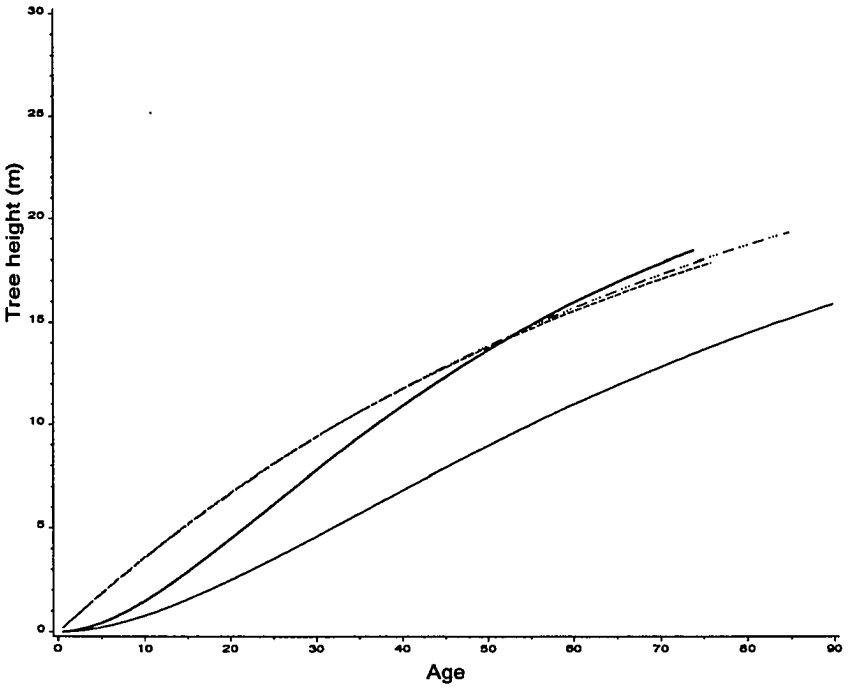


FIG. 46. Mean height growth in the **PIGL-BEPA/HYSP c.t.** Legend for species composition is: *Populus tremuloides* = ··· — ··· - ; *Betula papyrifera* = -------- ; Open-grown *Picea glauca* = ; Suppressed *Picea glauca* = ——— .

Comparison of productivity

Substantial variation in height growth of *P. glauca* exists between the five c.t.s (Fig. 47). At fifty years in total age, height ranges from about 10 m in the **POTR/SHCA c.t.** to 15 m in the **BEPA-POTR/VIED c.t.** *P. glauca* grows slowly in the **POTR/ARUV** and **POTR/SHCA c.t.s**. *P. glauca* in the **BEPA-POTR/VIED** and **PIGL-BEPA/HYSP c.t.s** have almost identical height growth patterns through the first forty years, after which *P. glauca* in the **BEPA-POTR/VIED c.t.** continues to increase in height and begins to level off in the **PIGL-BEPA/HYSP c.t.**

Height growth models for *P. glauca* in the five c.t.s (Fig. 47) constitute a set of polymorphic-nondisjoint curves because there is no constant proportionality relationship between different curves at the same age, and some of the curves intersect within the age range of interest. Furthermore, these curves constitute a substantial departure from Farr's (1967) anamorphic guide curves developed for pure, well-stocked stands. Only in the **POTR/SHCA** and **PIGL-BEPA/HYSP c.t.s** is height growth similar to that predicted by site index curves. Height growth of *P. glauca* in **POTR/SHCA c.t.** is similar parallel to that of site index class 60 and in the **PIGL-BEPA/HYSP c.t.** is similar to that of site index class 80. Quadratic mean diameters of all sample stands in the **POTR/SHCA c.t.** are less then those of pure, well-stocked stands of *P. glauca* of the same age and belonging to Farr's site class 60, indicating low productivity in this c.t.

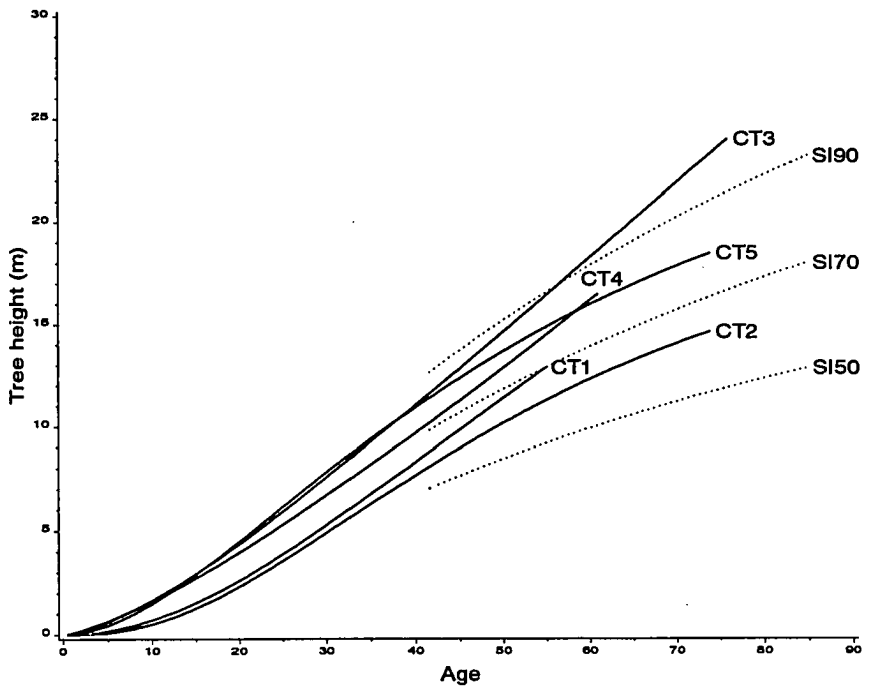


FIG. 47. Mean height growth of *Picea glauca* in five community types, and relationship to site index curves. CT1 = **POTR/ARUV c.t.**; CT2 = **POTR/SHCA c.t.**; CT3 = **BEPA-POTR/VIED c.t.**; CT4 = **BEPA-POTR/ALCR c.t.**; CT5 = **PIGL-BEPA/HYSP c.t.** Site index curves from Farr (1967).

Quadratic mean diameters of sample stands in the **PIGL-BEPA/HYSP c.t.** are not closely correlated with stand age. Several mixed stands contained stems with larger breast height quadratic mean diameters than those predicted for site class 80; a few stands had smaller quadratic mean diameters. No apparent difference existed between the associated vegetation in sample stands with higher quadratic mean diameter and the associated vegetation in sample stands with lower quadratic mean diameter in the **PIGL-BEPA/HYSP c.t.** Similar comparisons of productivity in the **POTR/ARUV**, **BEPA-POTR/VIED** and **BEPA-POTR/ALCR c.t.s** to productivity in pure, even-aged, fully stocked *P. glauca* stands are not available.

Height growth of *P. tremuloides* varies substantially between the five c.t.s (Fig. 48). At fifty years total age, *P. tremuloides* is slightly more than 10 m in height in the **POTR/ARUV c.t.** and almost 16 m in height in the **BEPA-POTR/VIED c.t.** Height growth of *P. tremuloides* in the **POTR/SHCA** is nearly identical at all ages to height growth in the **PIGL-BEPA/HYSP c.t.** These two c.t.s represent an intermediate level of productivity.

Like the models for *P. glauca*, height growth models for *P. tremuloides* in the five c.t.s (Fig. 48) constitute a set of polymorphic-nondisjoint curves because there is no constant proportionality relationship between different curves at the same age, and some of the curves intersect within the age range of interest. The *P. tremuloides* model of height growth in the **BEPA-POTR/ALCR c.t.**

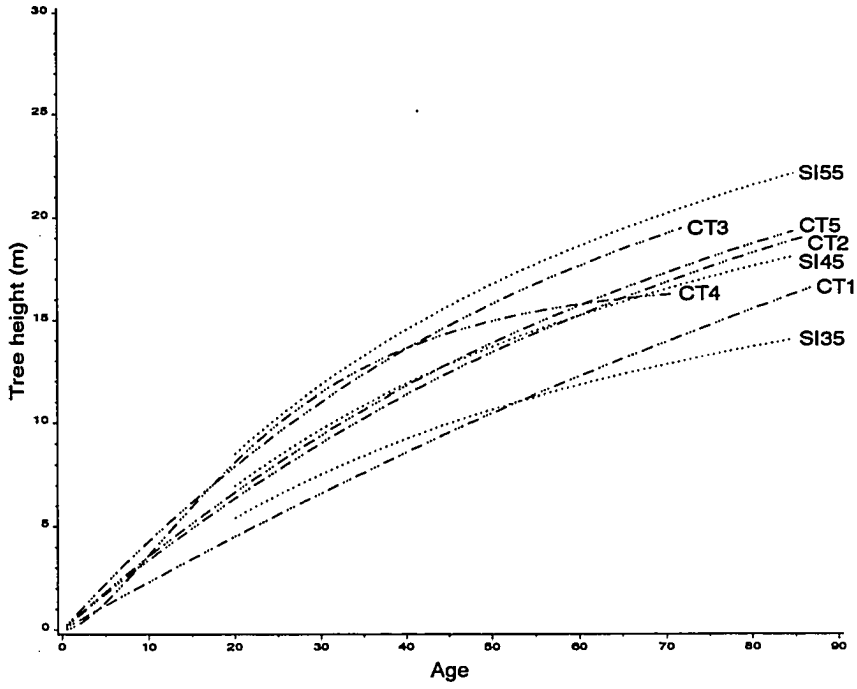


FIG. 48. Mean height growth of *Populus tremuloides* in five community types, and relationship to site index curves. CT1 = **POTR/ARUV c.t.**; CT2 = **POTR/SHCA c.t.**; CT3 = **BEPA-POTR/VIED c.t.**; CT4 = **BEPA-POTR/ALCR c.t.**; CT5 = **PIGL-BEPA/HYSP c.t.** Site index curves from Gregory and Haack (1965).

crosses three other curves. Height growth curves for four c.t.s differ in shape from anamorphic guide curves developed for pure, well-stocked stands. Only in the **BEPA-POTR/VIED c.t.** is height growth of *P. tremuloides* similar to that predicted by site index curves; height growth in this c.t. is roughly parallel to that of site index class 55 (Gregory and Haack 1965). Quadratic mean diameters of most sample stands in the **BEPA-POTR/VIED c.t.** are slightly less that those of pure, well-stocked stands of *P. tremuloides* of the same age belonging to site index class 55. Variation is such that site index class 55 is a reasonably good approximation of the upper limit of productivity in this c.t.

Height growth modes for *B. papyrifera* were developed only for the **BEPA-POTR/VIED, BEPA-POTR/ALCR** and **PIGL-BEPA/HYSP c.t.s** (Fig. 49). *B. papyrifera* has similar variation in maximum height growth within the three c.t.s compared to *P. glauca* and *P. tremuloides*. Within the three c.t.s, the range of height growth for *B. papyrifera* at 50 years total age is less than 2 m. The **BEPA-POTR/VIED c.t.** is the only c.t. for which a comparison to productivity of pure stands can be made on the basis of height growth of *B. papyrifera*. The curve for predicted height growth of *B. papyrifera* for this c.t. is less than and parallel to the guide curve of site index class 55 (Gregory and Haack 1965). Quadratic mean diameters for sample plots within this c.t. are similar to those predicted for pure, well-stocked site class 55 *B. papyrifera* stands of the same age, indicating that in this c.t. height of *B. papyrifera* is a reasonable predictor

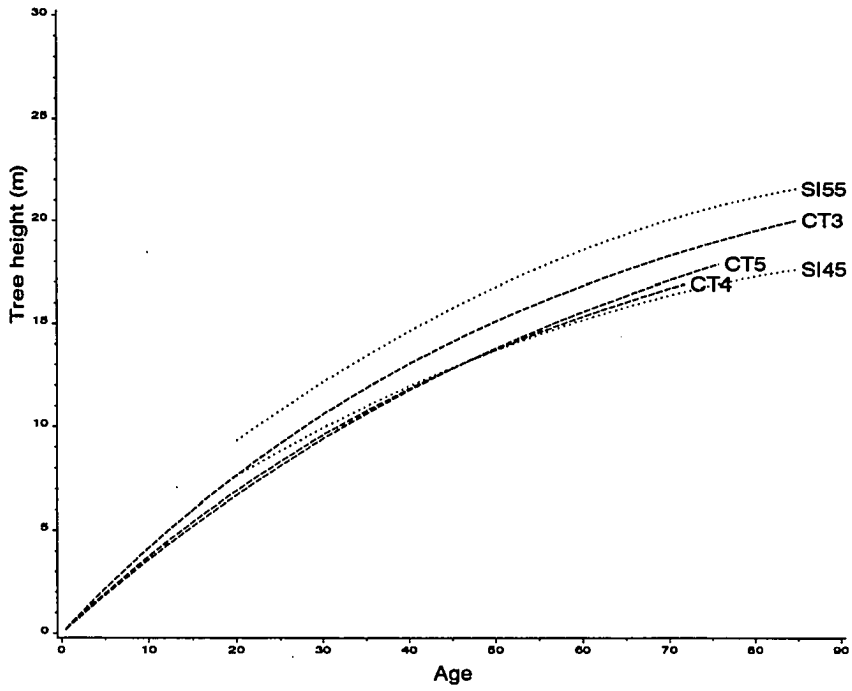


FIG. 49. Mean height growth of *Betula papyrifera* in three community types, and relationship to site index curves. CT3 = **BEPA-POTR/VIED c.t.**; CT4 = **BEPA-POTR/ALCR c.t.**; CT5 = **PIGL-BEPA/HYSP c.t.** Site index curves from Gregory and Haack (1965).

of productivity. Mixed stands represented by the **BEPA-POTR/VIED c.t.**, therefore, should have productivity approximating that of pure stands belonging to *B. papyrifera* site class 55.

Height growth models for *B. papyrifera* in the three c.t.s (Fig. 49) constitute a set of polymorphic-nondisjoint curves because there is no constant proportionality relationship between different curves at the same age, and the curves for the **BEPA-POTR/ALCR** and **PIGL-BEPA/HYSP c.t.s** intersect at 45 years of age. These curves differ from anamorphic or harmonized guide curves developed for pure, well-stocked stands of *B. papyrifera* (Gregory and Haack 1965).

Validation of classification

Data from 12 stands, collected independently of this study by other researchers, were used to validate the classification. One stand with *P. tremuloides* and *P. glauca* was on a moderately steep southeasterly slope in the southwestern portion of the study area; it contained over 70 percent combined cover of *Shepherdia canadensis, Viburnum edule* and *Linnaea borealis*, meeting the criteria for belonging to the **POTR/SHCA c.t.**

Seven stands were keyed to the **BEPA-POTR/VIED c.t.** and fell within the typal concept of geographical and environmental distribution and species composition. These stands had upper or midslope positions with aspects

ranging from southeast to west, elevations ranging from 210 to 335 m and a mean canopy cover of 13 percent for *Viburnum edule*.

One stand clearly belonged to the **BEPA-POTR/ALCR c.t.** based on overstory and undergrowth composition and physiography. One stand keyed to the same c.t., but may represent a variant between the **BEPA-POTR/ALCR c.t.** and the **PIGL-BEPA/HYSP c.t.** because it contained slightly more than five percent canopy cover in *Alnus crispa* and over 70 percent cover in *Hylocomium splendens*. Additional site information and compositional data available in the field would clarify placement.

Two additional stands, one dominated by *P. glauca* and one by *B. papyrifera*, met the typal concept of the **PIGL-BEPA/HYSP c.t.** These data substantiate the relative ease in which stands may be classified to their respective c.t.s, and substantiate the distribution of these c.t.s beyond the stands used in their construction.

CONCLUSIONS AND RECOMMENDATIONS

This study of forest stand development in young, mixed stands was conducted to refine current concepts of forest community succession on upland sites. Area of consideration was restricted to a relatively narrow portion of the ecological spectrum for upland forests in interior Alaska: warm and dry sites supporting productive mixed hardwood and *Picea glauca* stands. Specific objectives were: *i*) describe the structural characteristics of young mixed hardwood-conifer stands, including composition, horizontal and vertical arrangement and component size; *ii*) define common stand development patterns; *iii*) compare juvenile height and diameter growth increment for the different species; *iv*) correlate existing stand structure with stand-disturbing events; and *v*) suggest various considerations for manipulating stand structure and composition of mixed stands to maintain productivity and provide a variety of forest products.

Structural characteristics of young mixed stands are described in terms of community types (c.t.s) and time since stand-replacing disturbance. A c.t. is an abstract grouping of all similar plant communities. C.t.s form a classification tool for partitioning overall variability in species composition within the study area into discrete, recognizable and mappable units of vegetation. Time since stand-replacing disturbance was based on total age of component stems.

Direct comparison of physical characteristics between c.t.s should not be made without caution, nor was it an objective of the study. C.t.s are defined on the basis of relative abundance of differential species in the undergrowth. Composition of individual stands may be compared on the basis of these species and their relative ecological amplitude, with individual species acting as phytometers. Certain key and easily measured physical characteristics of sites, such as slope, aspect, elevation and perhaps Latitude of Equivalent Slope, are likely to influence species composition, and therefore influence the classification of c.t.s. Slope, aspect, elevation and latitude of Equivalent Slope do not form a finite set of ecological parameters, however, and plants are likely to react to the interaction of these and other undefined physical characteristics.

Structural characteristics, including species composition within crown strata, density of living and dead stems by diameter class, quadratic mean diameter, basal area, canopy height, crown size and spatial arrangement of stems, were described by c.t. These characteristics vary between and within c.t.s (appendix F). In general, the **POTR/ARUV c.t.** includes stands with many small-diameter *Populus tremuloides* and an undergrowth dominated by low shrubs. These stands occur on relatively warm and dry, steep south-facing aspects. The **POTR/SHCA c.t.** occurs on more mesic sites, with an overstory dominated by *P. tremuloides* and an undergrowth dominated by various tall shrubs. Trees are larger and density is less than in the **POTR/ARUV c.t** for

stands of comparable age. The three remaining c.t.s occur on relatively cool, more moist sites, and differ in overall composition and structure. In both the **BEPA-POTR/VIED** and **BEPA-POTR/ALCR c.t.s**, *Betula papyrifera* is often a major component, sometimes sharing this role with *P. tremuloides*. Undergrowth structure and composition is dominated by tall shrubs. The **PIGL-BEPA/HYSP c.t.** has structural characteristics derived from dominance of *P. glauca* in the overstory and an herbaceous undergrowth with well-developed moss layers.

Patterns of stand development for each c.t. were derived from the mean number of years for establishment of different species in each stand and subsequent height and diameter growth, with establishment relative to total age of the oldest tree in each stand. Two types of developmental patterns were identified: *i*) rapid establishment of hardwoods with prolonged establishment of *P. glauca*, and *ii*) rapid and concurrent establishment of hardwoods and *P. glauca* (Table 11). In both the **POTR/ARUV** and **POTR/SHCA c.t.s**, the consistent pattern of development is rapid establishment of *P. tremuloides* following a stand-replacing disturbance, with slow, sporadic and occasional establishment of *P. glauca* occurring in a prolonged invasion. Subsequent growth of *P. glauca* is usually slow. The common pattern of development in the **BEPA-POTR/VIED**, **BEPA-POTR/ALCR** and **PIGL-BEPA/HYSP c.t.s** is rapid concurrent establishment of *B. papyrifera*, *P. tremuloides* and *P. glauca*

Table 11. Summary of stand development patterns, growth rates and type of succession by community type.

	POTR/ARUV	POTR/SHCA	BEPA-POTR/VIED	BEPA-POTR/ALCR	PIGL-BEPA/HYSP
Stand development pattern	Rapid establishment of Potr[1]; prolonged establishment of Pigl	Rapid establishment of Potr; prolonged establishment of Pigl	Rapid, concurrent establishment of Potr, Bepa and Pigl OR Rapid establishment of Potr and Bepa; prolonged establishment of Pigl	Rapid, concurrent establishment of Potr, Bepa and Pigl OR Rapid establishment of Potr and Bepa; prolonged establishment of Pigl	Rapid, concurrent establishment of Bepa and Pigl OR Rapid establishment of Potr and Bepa, prolonged establishment of Pigl
Projected density of Pigl	Low	Moderate	Moderate	Moderate	High
Relative growth rate of Potr	Low	Moderate	High	Moderate	Moderate
Relative growth rate of Bepa	NA[2]	NA	High	Moderate	Moderate
Relative growth rate of Pigl	Low	Low	High	Moderate	Moderate
Succession type[3]	Partial Tolerance	Partial Tolerance	Partial Inhibition and Tolerance	Partial Inhibition and Tolerance	Partial Inhibition and Tolerance

[1] Species codes: Potr = *Populus tremuloides*; Bepa = *Betula papyrifera*; Pigl = *Picea glauca*.
[2] NA = Species rarely occurs in c.t.
[3] From Connell and Slatyer 1977.

following a stand-replacing disturbance. In addition, these three c.t.s also include stands dominated by *B. papyrifera* and *P. tremuloides* in which establishment of *P. glauca* is not concurrent. Subsequent growth of both hardwoods and *P. glauca* is variable. Based on identification of these two patterns of development, the hypothesis of "conversion from hardwoods to conifers occurring through a gradual invasion of conifers in an even-aged hardwood stand" is rejected. First, the pattern of development for the **POTR/ARUV** and **POTR/SHCA c.t.s** is based on a difference between mean number of years for establishment in hardwoods compared to *P. glauca*. *P. glauca* does not continue to invade these hardwood stands as the hardwoods mature. The establishment of *P. glauca* is prolonged but not continual. A second reason for rejecting the hypothesis is that establishment of *P. glauca* in the **BEPA-POTR/VIED, BEPA-POTR/ALCR** and **PIGL-BEPA/HYSP c.t.s** is, in most cases, concurrent with hardwood establishment. For the few stands that are an exception, the previous rational also applies.

Patterns of development based on initial stem establishment, and subsequent height growth of component species through approximately 70 years, relate to future stand structure and composition. C.t.s with prolonged establishment of *P. glauca* generally have low *P. glauca* density. These stands show little indication of supporting higher densities of conifers in the future.

The c.t. classification resulting from this study serves as an initial resource

stratification system and a first approximation of relative productivity in mixed stands. A second hypothesis guiding this study was "productivity of *P. glauca* in mixed stands is equal to that of *P. glauca* in pure stands for similar sites." Based on models of height growth, *P. tremuloides*, *B. papyrifera* and *P. glauca* each grow differentially within the c.t.s. Differences in productivity between pure stands and mixed stands were estimated by comparing height growth curves from mixed stands to site index curves, and when similar curves were found, comparing the quadratic mean diameter of the pure stands to those of mixed stands of the same age. Because of dissimilar height growth curves, this hypothesis could only be considered for the **POTR/SHCA** and **PIGL-BEPA/HYSP c.t.s**. The hypothesis was rejected for both c.t.s; in the first c.t. because quadratic mean diameters are less than pure stands, and in the second because stem sizes are poorly correlated to stand age.

Because of diversity in species composition and differences in patterns of development within young mixed upland stands, identification of c.t. is a prerequisite for selecting the target species or group of species to feature in silvicultural manipulations (Table 11). With inconsistent natural regeneration of *P. glauca* in the **POTR/ARUV** and **POTR/SHCA c.t.s**, silvicultural manipulations of these stands should be limited to those featuring *P. tremuloides* as the target species. This approach was reviewed in detail for similar stands in Canada (Navratil *et al.* 1991). These workers concluded that short rotations, such as 50

to 100 years, and short planning cycles, such as 5-year funding-renewal horizons, encourage reliance on extensive, even-aged management of monocultures.

Opportunities for stand manipulation to achieve objectives of mixed stand management, such as better utilization of wood-growing potential of a site, and better stand stability by preventing monocultures, may best be realized in the **BEPA-POTR/VIED c.t.** In this c.t., relatively high rates of growth are common to all three principal species. Navratil *et al.* (1991) presented a model for a two-stage silvicultural system for management of mixed stands that may be applicable for sites supporting this c.t. Their model involves harvesting hardwoods and *P. glauca* at different times with prompt natural regeneration of all species controlled by some form of seed tree retention. Productivity and economics of managing mixed hardwood stands with *Picea abies* (L.) Karst. is reviewed by Frivold (1985) and Frivold and Mielikäinen (1990). Day and Bell (1988) provide a comparable discussion for mixed stands in Ontario, Canada. A common theme throughout this work in Fennoscandia and Canada is that management of mixed stands is more difficult, more costly and more unpredictable than management of pure stands.

Succession is not easy to characterize within the five c.t.s described in this study (Table 11). There are three general models of secondary succession: the facilitation or relay floristics model, the initial floristics or tolerance model and

the inhibition model (Connell and Slatyer 1977, Miles 1979). The facilitation model involves a directional and deterministic change, with each successive plant community the result of site modifications by the previous plant community. The initial florists or tolerance model assumes that all species present in later communities are present following the initial disturbance or immigrate in, and suggests that initial community composition and subsequent changes are the result of different rates of growth, reproduction and survival. Replacement of species occurs because of an interaction of stress tolerance and competition. This model is probabilistic in that no two plant communities will be exactly the same. The inhibition model suggests that a particular plant community, once developed, can inhibit further succession by excluding or suppressing further occupancy through physical occupancy of the site, monopolization of light, moisture or nutrients, or production of allelopathic substances.

P. tremuloides acts to suppress growth of new suckers within a stand through apical dominance in the **POTR/ARUV** and **POTR/SHCA c.t.s**. *P. tremuloides* and *B. papyrifera* if present, act to suppress the growth of slowly establishing *P. glauca*. There is little evidence, however, that either species modifies the environment so that conditions are either more or less suitable for establishment of *P. glauca*. Establishment of *P. glauca* after *B. papyrifera*, such as in stands 35 and 53 (Figs. 17 and 45), refutes the notion of Gregory (1966)

that smothering or crushing of seedlings by fallen leaves prevented establishment of all but an occasional *P. glauca*. Lacking evidence for either enhanced or impaired site conditions, the facilitation and inhibition models of succession are rejected. The tolerance model represents successional changes in these c.t.s, at least in part, because *P. glauca* becomes established after the hardwoods. The tolerance model fits only partially because *P. glauca* apparently does not continue to invade established hardwood stands. The underlying assumption of homogeneity of the environment in all three models of succession is violated in the **POTR/ARUV** and **POTR/SHCA c.t.s** if these types represent ecotonal environments for *P. glauca* because it becomes established only in years of above-normal moisture availability.

In contrast, the **BEPA-POTR/VIED, BEPA-POTR/ALCR** and **PIGL-BEPA/HYSP c.t.s** develop most often from rapid and concurrent establishment of all species, with little or no subsequent establishment. This pattern is best represented by the inhibition model because there is little change in species composition after initial establishment. Both *B. papyrifera* and *P. glauca* remain in the stand because of longevity. Stands not characterized by this pattern were noted, however, indicating the tolerance model does not describe completely the successional relations in this c.t.

Previous work (Van Cleve and Viereck 1981, Van Cleve *et al.* 1991) has relied on the facilitation model to describe successional trends in upland mixed

stands. Their work suggested that successional changes were deterministic, culminating in the dominance of *P. glauca*. Key features of the facilitation model, as applied to these upland mixed stands, include gradual changes in burned forest floor and surface layers of mineral soil as a result of leaching, nitrification and ion uptake, and establishment of a bryophyte ground cover coincident with the accumulation of leaf litter (Van Cleve *et al.* 1991). Conversion of hardwood stands to stands dominated by *P. glauca* was attributed to the shorter life-span and shade intolerance of these species. In this study, examination of only a relatively short segment of the potential successional time gradient indicates that in some c.t.s, conversion of hardwood stands to stands dominated by *P. glauca* is not *a priori*.

The three general models of succession offered by Connell and Slatyer (1977) should be considered summaries of state-of-the-art theory developed from well-understood and ideal systems. As such, they represent targets for hypothesis testing and rejection as these theories are extrapolated to new and different ecosystems. Patterns of stand development in this portion of the boreal forest suggest that rigorous hypothesis testing would lead to model rejection, and the need for synthesis of a new model to describe the successional pathways.

This study points out the difficulties in estimating site quality for sites supporting pure stands compared to sites supporting mixed stands, and

provides one technique for overcoming this difficulty. Identification of open-grown trees free of competition in mixed stands will continue to hamper development of management guides for these stands.

Finally, this study is the first to consider the spatial arrangement of stems in young mixed stands in this portion of the boreal forest. Although not expressly quantified, it indicates the variability in spatial arrangement by species and stem sizes. Opportunities are immense for future research to identify patterns in the spatial arrangement of stems in these stands and the underlying causes for spatial patterns.

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APPENDICES

APPENDIX A.--TAXONOMIC NOMENCLATURE FOR PLANT SPECIES OBSERVED IN THIS STUDY

TREES

Betula papyrifera Marsh.

Picea glauca (Moench) Voss

Picea mariana (Mill.) Britt., Sterns & Pogg.

Populus balsamifera L.

Populus tremuloides Michx.

SHRUBS

Alnus crispa (Ait.) Pursh

Amelanchier alnifolia (Nutt.) Nutt.

Arctostaphylos uva-ursi (L.) Spreng.

Empetrum nigrum L.

Juniperus communis L.

Ledum palustre L.

Linnaea borealis L.

Potentilla fruticosa L.

Ribes triste Pall.

Rosa acicularis Lindl.

Salix alaxensis (Anderss.) Cov.

Salix glauca L.

Salix scouleriana Barratt

Sambucus racemosa L.

Shepherdia canadensis (L.) Nutt.

Spiraea beauverdiana Schneid.

Vaccinium uliginosum L.

Vaccinium vitis-idaea L.

Viburnum edule (Michx.) Raf.

FORBS

Actaea rubra (Ait.) Willd.

Apocynum androsaemifolium L.

Cnidium cnidiifolium (Turcz.) Schischk.

Cornus canadensis L.

Cypripedium guttatum Sw.

Delphinium glaucum S. Wats.

Epilobium angustifolium L.

Galium boreale L.

Geocaulon lividum (Richards.) Fern.

Geranium bicknellii Britt.

Goodyera repens (L.) R. Br.

Hedysarum alpinum L.

Mertensia paniculata (Ait.) G. Don

Moehringia lateriflora (L.) Fenzl

Polygonum alaskanum (Small) Wight

Pulsatilla patens (L.) Mill.

Pyrola asarifolia Michx.

Pyrola secunda L.

Thalictrum sparsiflorum Turcz.

Zygadenus elegans Pursh

GRAMINOIDS

Bromus pumpellianus Scribn.

Calamagrostis canadensis (Michx.) Beauv.

Deschampsia caespitosa (L.) Beauv.

Festuca altaica Trin.

MOSSES AND ALLIES

Equisetum arvense L.

Eurhynchium stokesii (Turn.) B.S.G.

Hylocomium splendens (Hedw.) B.S.G.

Lycopodium annotinum L.

Lycopodium complanatum L.

Peltigera aphthosa (L.) Willd.

Pleurozium schreberi (Brid.) Mitt.

Ptilium crista-castrensis (Hedw.) De Not.

Rhytidium rugosum (Hedw.) Kindb.

Rhytidiadelphus triquetrus (Hedw.) Warnst.

APPENDIX B.--CLIMATIC CHARACTERISTICS OF THE STUDY AREA

	Temperature °C						Precipitation					
	Mean maximum			Mean minimum			Mean total (mm)			Snowfall (cm)		
Month	FB[1]	NE[2]	BC[3]	FB	NE	BC	FB	NE	BC	FB	NE	BC
Jan.	-20	-21	-19	-30	-32	-23	17.0	11.2	NA	24.6	NA[4]	NA
Feb.	-14	-24	-14	-26	-37	-19	11.7	17.8	NA	22.1	NA	NA
Mar.	-6	-3	-6	-21	-15	-14	9.9	4.8	NA	15.5	NA	NA
Apr.	5	9	4	-7	-4	-4	7.1	3.3	NA	8.6	NA	NA
May	15	20	12	3	3	5	16.8	5.8	29.3	1.3	NA	NA
Jun.	21	22	18	9	8	11	35.3	40.6	88.1	0	NA	NA
Jul.	22	24	18	11	11	11	47.5	74.9	102.3	0	NA	NA
Aug.	19	21	16	8	8	9	54.9	90.4	104.5	0	NA	NA
Sep.	12	10	10	2	2	1	26.2	49.3	42.0	2.3	NA	NA
Oct.	0	NA	-2	-8	NA	-7	22.3	NA	NA	27.4	NA	NA
Nov.	-11	-16	-15	-20	-25	-19	17.8	51.3	NA	34.3	NA	NA
Dec.	-19	NA	-10	-28	NA	-17	17.5	NA	NA	34.3	NA	NA
Annual	2	4	1	-9	-8	-5	284	350	NA	169.9	NA	NA

[1] Fairbanks Airport: lat. 64°49'N, long. 147°52'W, elevation 133 meters, record = 1961 to 1990.
[2] Nenana Municipal Airport: lat. 64°33'N, long. 149°05'W, elevation 109 meters, record = 1961 to 1990.
[3] Bonanza Creek Experimental Forest: lat. 64°45'N, long. 148°19'W, elevation 335 meters, record = Oct 1987 to 1991 for temperature, 1988 to 1991 for precipitation.
[4] Data Not Available

APPENDIX C.--KEY TO THE COMMUNITY TYPES

This key to upland mixed hardwood-conifer community types is provided as an aid to the identification of communities within or adjacent to the Fairbanks-Big Delta area of the Yukon-Tanana uplands. It is oniy applicable on sites supporting young stands of hardwoods and conifer in which *Picea mariana* is not a dominant component.

1. *Arctostaphylos uva-ursi* at least 5 percent cover, usually much greater; *Shepherdia canadensis* always present; *Juniperus communis* sometimes present . . . . . **Populus tremuloides/Arctostaphylos uva-ursi c.t.** (p. 57)

1. Not as above . . . . . 2.

2. *Shepherdia canadensis* and *Viburnum edule* both at least 5 percent cover; *Geocaulon lividum* usually at least 5 percent cover; *Arctostaphylos uva-ursi* absent; *Linnaea borealis* usually present . . . . . **Populus tremuloides/Shepherdia canadensis c.t.** (p. 78)

2. Not as above . . . . . 3.

3. *Viburnum edule* and/or *Linnaea borealis* at least 5 percent cover; *Geocaulon lividum* usually absent . . . . . **Betula papyrifera-Populus tremuloides/Viburnum edule c.t.** (p. 95)

3. Not as above . . . . . 4.

4. *Alnus crispa* usually at least 5 percent cover; *Calamagrostis canadensis* sometimes at least 50 percent cover; cover of mosses often highly variable . . . . . **Betula papyrifera-Populus tremuloides/Alnus crispa c.t.** (p. 119)

4. *Alnus crispa* usually less than 5 percent cover; feathermosses such as *Hylocomium splendens* or *Rhytidium rugosum* usually at least 50 percent cover; *Equisetum arvense* usually more than 5 percent cover; *Calamagrostis canadensis* usually absent . . . . . **Picea glauca-Betula papyrifera/Hylocomium splendens c.t.** (p. 140)

APPENDIX D.--PHYSICAL CHARACTERISTICS OF STANDS BY COMMUNITY TYPE

POTR/ARUV c.t						
Stand	Latitude	Longitude	Elevation (m)	Aspect (°)	Slope (%)	LES[1]
21	64°35'14	149°04'15	412	160	53	35.5
12	64°34'15	149°04'45	183	186	23	51.7
49	65°28'37	148°09'59	259	160	43	43.0
48	65°17'36	148°09'07	274	170	55	36.7
11	64°39'23	148°30'57	168	160	45	41.2
44	64°38'53	148°42'50	152	180	25	50.6
10	64°39'35	148°30'38	152	126	27	53.8
POTR/SHCA c.t						
Stand	Latitude	Longitude	Elevation (m)	Aspect (°)	Slope (%)	LES
35	64°54'32	148°19'06	305	180	35	47.1
9	64°35'04	148°54'46	168	237	16	58.7
36	64°51'44	147°00'02	183	160	4	62.7
24	64°44'41	148°24'33	274	190	10	59.1
45	64°36'15	148°41'03	213	170	5	61.2
14	64°43'19	148°33'46	274	147	17	56.2
19	64°43'36	148°33'07	305	186	10	59.0
8	64°40'31	148°51'41	251	146	28	50.8

(Cont.)

BEPA-POTR/VIED c.t						
Stand	Latitude	Longitude	Elevation (m)	Aspect (°)	Slope (%)	LES
42	64°54'35	148°13'32	198	195	25	51.2
55	64°52'18	147°49'03	149	100	2	64.6
20	64°35'18	149°04'31	457	255	40	52.9
6	64°42'28	148°19'22	183	170	21	53.4
5	64°44'13	148°14'24	175	276	20	63.6
29	64°54'00	147°01'29	305	310	2	65.6
37	64°18'23	146°32'24	457	184	35	45.0
50	65°19'58	148°18'54	198	225	5	63.2
32	64°50'51	147°03'10	320	152	18	55.5
39	64°54'32	148°19'06	305	180	35	45.6
18	64°42'34	148°34'34	259	220	10	60.1
16	64°42'38	148°34'22	259	105	8	63.2
13	64°43'54	148°42'53	244	265	15	62.7
30	64°33'15	146°50'19	280	30	5	70.0
BEPA-POTR/ALCR c.t						
Stand	Latitude	Longitude	Elevation (m)	Aspect (°)	Slope (%)	LES
3	65°10'36	147°28'32	335	136	16	58.0
2	65°11'59	147°29'02	579	220	19	56.3
4	64°45'57	148°19'07	381	200	15	56.6
27	64°54'08	147°01'56	381	248	28	56.0
28	64°54'14	147°01'04	351	210	30	49.6
43	64°54'04	148°14'02	229	132	15	58.6
38	64°18'23	146°33'20	518	75	30	63.6
51	65°07'02	147°37'57	518	166	25	51.4

(Cont.)

BEPA-POTR/ALCR c.t (cont.)						
Stand	Latitude	Longitude	Elevation (m)	Aspect (°)	Slope (%)	LES
47	65°17'57	148°10'07	351	190	10	59.6
52	65°06'27	147°37'17	244	166	20	54.0
41	64°54'08	148°15'16	259	210	10	59.8
33	64°51'23	147°01'35	320	72	55	58.9
31	64°19'42	146°45'04	290	190	5	61.5
PIGL-BEPA/HYSP c.t						
Stand	Latitude	Longitude	Elevation (m)	Aspect (°)	Slope (%)	LES
1	65°10'48	147°31'02	427	80	24	64.1
7	64°42'38	148°18'25	198	52	25	63.6
53	65°06'37	147°42'02	305	160	10	59.7
46	64°39'45	148°39'50	213	0	0	64.6
40	64°54'31	148°17'46	305	180	5	62.0
34	64°50'16	147°01'51	305	90	7	64.5
22	64°42'46	148°33'46	274	130	5	62.8
17	64°42'26	148°34'29	244	104	7	63.5
15	64°41'35	148°34'19	198	184	5	61.8
23	64°42'55	148°28'37	229	130	15	58.6
54	64°52'18	147°49'36	152	82	5	65.1

[1] Latitude of Equivalent Slope, in degrees

APPENDIX E.--CONSTANCY AND AVERAGE COVER (IN PARENTHESES) OF IMPORTANT PLANTS BY COMMUNITY TYPE

	POTR-ARUV	POTR/SHCA	BEPA-POTR/VIED	BEPA-POTR/ALCR	PIGL-BEPA/HYSP
NO. STANDS IN C.T.:	7	8	14	13	11
TREES					
BETULA PAPYRIFERA <5cm	29(6)	25(T)	50(11)	85(7)	45(11)
BETULA PAPYRIFERA 5-15cm	14(10)	13(15)	64(37)	92(32)	55(24)
BETULA PAPYRIFERA >15cm	14(20)	-(-)	57(36)	85(36)	73(26)
PICEA GLAUCA <5cm	86(9)	100(8)	86(5)	54(8)	82(8)
PICEA GLAUCA 5-15cm	86(9)	88(28)	93(16)	54(16)	82(30)
PICEA GLAUCA >15cm	43(10)	50(14)	64(14)	31(7)	73(40)
PICEA MARIANA <5cm	-(-)	13(3)	7(5)	38(13)	27(3)
PICEA MARIANA 5-15cm	-(-)	13(5)	7(10)	23(2)	9(15)
PICEA MARIANA >15cm	-(-)	-(-)	-(-)	15(3)	-(-)
POPULUS BALSAMIFERA <5cm	71(2)	13(T)	7(2)	8(T)	-(-)
POPULUS BALSAMIFERA 5-15cm	43(7)	25(8)	7(5)	-(-)	9(5)
POPULUS BALSAMIFERA >15cm	-(-)	13(5)	7(30)	-(-)	-(-)
POPULUS TREMULOIDES <5cm	100(23)	100(7)	43(6)	15(3)	18(3)
POPULUS TREMULOIDES 5-15cm	100(36)	100(47)	57(41)	62(28)	55(15)
POPULUS TREMULOIDES >15cm	57(23)	100(37)	43(33)	46(29)	55(24)
TALL SHRUBS					
ALNUS CRISPA	14(2)	25(18)	57(15)	100(33)	55(7)
AMELANCHIER ALNIFOLIA	29(2)	13(2)	-(-)	-(-)	-(-)
LEDUM PALUSTRE	-(-)	13(25)	21(1)	46(4)	27(4)
RIBES TRISTE	-(-)	-(-)	-(-)	8(T)	-(-)
ROSA ACICULARIS	86(8)	100(11)	93(10)	77(4)	100(3)
SALIX GLAUCA	-(-)	25(8)	-(-)	15(1)	9(15)
SALIX SCOULERIANA	29(10)	13(5)	14(8)	15(20)	9(T)
SALIX SPECIES	-(-)	13(2)	21(4)	8(T)	9(2)
SHEPHERDIA CANADENSIS	100(30)	100(30)	14(1)	-(-)	9(T)
SPIRAEA BEAUVERDIANA	-(-)	-(-)	-(-)	15(13)	-(-)
VACCINIUM ULIGINOSUM	-(-)	-(-)	-(-)	23(7)	18(1)
VIBURNUM EDULE	71(21)	100(18)	100(18)	46(4)	64(1)
LOW SHRUBS					
ARCTOSTAPHYLOS UVA-URSI	100(51)	-(-)	-(-)	-(-)	-(-)
JUNIPERUS COMMUNIS	29(20)	-(-)	-(-)	-(-)	-(-)
LINNAEA BOREALIS	57(14)	88(21)	71(29)	62(2)	73(2)
VACCINIUM VITIS-IDAEA	-(-)	25(42)	36(22)	54(6)	55(13)
FORBS					
ACTAEA RUBRA	-(-)	-(-)	7(T)	-(-)	-(-)
APOCYNUM ANDROSAEMIFOLIUM	29(20)	-(-)	-(-)	-(-)	-(-)
CASTILLEJA SPECIES	14(T)	-(-)	-(-)	-(-)	-(-)
CNIDIUM CNIDIIFOLIUM	57(1)	25(3)	-(-)	-(-)	-(-)

(cont.)

APPENDIX E.--(Con.)

NO. STANDS IN C.T.:	POTR-ARUV 7	POTR/SHCA 8	BEPA-POTR/VIED 14	BEPA-POTR/ALCR 13	PIGL-BEPA/HYSP 11
FORBS (Cont.)					
CORNUS CANADENSIS	43(5)	50(8)	64(6)	38(6)	36(1)
CYPRIDEDIUM SPECIES	14(20)	-(-)	-(-)	-(-)	-(-)
DELPHINIUM GLAUCUM	14(T)	-(-)	-(-)	-(-)	-(-)
EPILOBIUM ANGUSTIFOLIUM	57(2)	100(5)	79(3)	54(1)	27(2)
ERIGERON SPECIES	14(T)	-(-)	-(-)	-(-)	-(-)
GALIUM BOREALE	100(7)	88(6)	21(1)	8(2)	18(T)
GEOCAULON LIVIDUM	71(3)	100(10)	21(1)	46(1)	36(1)
GOODYERA REPENS	-(-)	-(-)	-(-)	-(-)	18(T)
MERTENSIA PANICULATA	-(-)	63(1)	43(1)	23(2)	64(1)
MOEHRINGIA LATERIFLORA	14(T)	-(-)	7(1)	8(3)	9(T)
PYROLA ASARIFOLIA	-(-)	13(T)	14(3)	15(1)	9(T)
PYROLA SECUNDA	29(1)	38(1)	29(2)	31(T)	36(T)
SOLIDAGO SPECIES	14(1)	-(-)	7(T)	-(-)	-(-)
ZIGADENUS ELEGANS	71(1)	25(1)	7(T)	-(-)	-(-)
MOSS AND ALLIES					
DICRANUM SPECIES	-(-)	-(-)	-(-)	8(T)	-(-)
EQUISETUM ARVENSE	29(T)	75(1)	86(19)	23(5)	73(31)
EURHYNCHIUM SPECIES	-(-)	-(-)	-(-)	8(T)	-(-)
FOLIOSE LICHENS	-(-)	-(-)	-(-)	-(-)	9(5)
HYLOCOMIUM SPLENDENS	-(-)	25(13)	57(10)	77(4)	82(46)
LYCOPODIUM ANNOTINUM	-(-)	-(-)	-(-)	15(1)	-(-)
LYCOPODIUM COMPLANATUM	-(-)	-(-)	7(5)	15(26)	9(50)
LYCOPODIUM SPECIES	-(-)	25(1)	36(10)	38(13)	-(-)
MOSS SPECIES	-(-)	38(1)	7(15)	8(1)	-(-)
PELTIGERA APHTHOSA	-(-)	-(-)	-(-)	15(1)	9(T)
PLEUROZIUM SCHREBERI	-(-)	-(-)	-(-)	8(T)	-(-)
POLYTRICHUM SPECIES	-(-)	-(-)	-(-)	8(T)	-(-)
PTILIUM CRISTA-CASTRENSIS	-(-)	-(-)	-(-)	8(T)	-(-)
RHYTIDIUM RUGOSUM	-(-)	-(-)	-(-)	-(-)	18(89)
GRAMINOIDS					
BROMUS SPECIES	86(2)	-(-)	-(-)	-(-)	-(-)
CALAMAGROSTIS CANADENSIS	43(1)	63(4)	86(8)	69(23)	18(1)
FESTUCA ALTAICA	14(T)	-(-)	-(-)	-(-)	-(-)

APPENDIX F.--STRUCTURAL CHARACTERISTICS OF STANDS BY COMMUNITY TYPE

Stand	Age[1]	Canopy height[2] (m)	QMD[3] (cm)	Density (trees per hectare)	Basal area (m^2 per hectare)
POTR/ARUV c.t.					
21	58	6.4	3.3	4,293	3.7
12	58	12.3	7.6	4,027	12.6
49	58	8.9	5.5	5,840	14.4
48	65	10.3	6.8	3,280	12.0
11	66	13.1	5.2	3,733	7.9
44	71	13.9	9.8	2,533	19.1
10	87	20.3	11.6	1,200	12.6
POTR/SHCA c.t.					
Stand	Age	Canopy height (m)	QMD (cm)	Density (trees per hectare)	Basal area (m^2 per hectare)
35	66	15.2	10.9	2,240	20.8
9	72	20.2	14.4	1,253	20.5
36	72	14.2	8.9	3,547	22.2
24	75	18.0	12.0	2,293	26.1
45	78	16.4	10.9	2,960	27.6
14	86	22.1	16.6	2,187	47.2
19	86	19.4	11.5	2,267	23.4
8	93	NA[4]	14.3	1,867	29.9

(Cont.)

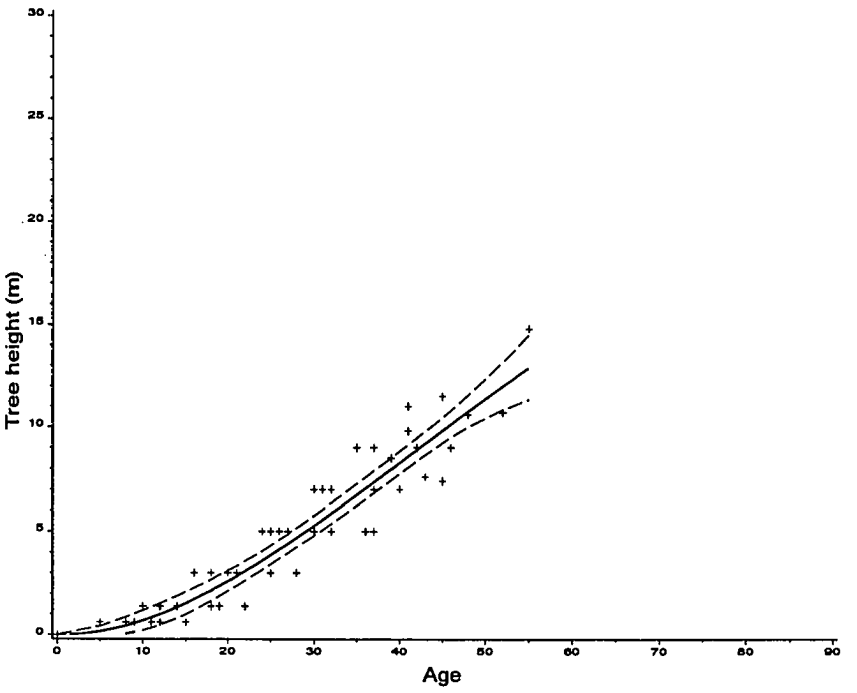
BEPA-POTR/VIED c.t.					
Stand	Age	Canopy height (m)	QMD (cm)	Density (trees per hectare)	Basal area (m^2 per hectare)
42	46	11.9	6.8	6,427	23.6
55	53	18.1	11.3	2,533	25.5
20	54	12.3	19.8	5,040	22.7
6	56	17.5	9.2	4,187	26.4
5	63	17.5	8.3	2,987	16.0
29	63	25.0	16.7	2,187	47.9
37	64	19.2	16.9	853	19.1
50	66	11.9	8.5	2,907	16.4
32	70	15.0	10.7	3,147	28.4
39	72	23.6	13.2	2,320	31.5
18	74	18.5	13.7	2,213	32.4
16	75	18.8	15.0	1,333	23.7
13	82	18.4	16.0	1,467	29.5
30	136	21.5	19.8	773	23.8
BEPA-POTR/ALCR c.t.					
Stand	Age	Canopy height (m)	QMD (cm)	Density (trees per hectare)	Basal area (m^2 per hectare)
3	59	15.0	14.1	1,123	17.5
2	61	17.3	10.2	3,573	29.4
4	62	18.3	12.9	2,400	31.2
27	62	16.2	10.6	2,907	25.7
28	63	14.5	8.4	4,107	22.7
43	63	16.1	9.2	3,440	23.3
38	63	16.4	13.5	1,813	26.0

(Cont.)

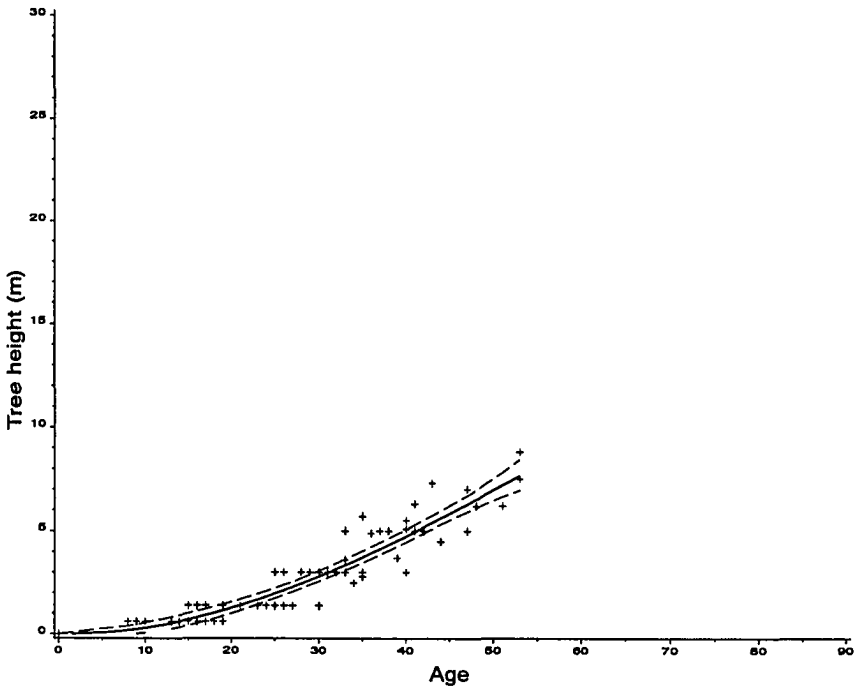
BEPA-POTR/ALCR c.t. (cont.)					
Stand	Age	Canopy height (m)	QMD (cm)	Density (trees per hectare)	Basal area (m^2 per hectare)
51	65	12.8	12.6	1,520	19.0
47	65	14.5	10.8	1,253	11.5
52	65	17.2	16.7	960	20.8
41	71	15.2	14.5	987	16.2
33	71	17.9	9.3	3,227	21.7
31	141	23.0	16.9	1,227	27.5
PIGL-BEPA/HYSP c.t.					
Stand	Age	Canopy height (m)	QMD (cm)	Density (trees per hectare)	Basal area (m^2 per hectare)
1	58	13.5	10.4	2,960	25.3
7	63	17.5	8.2	1,573	8.3
53	64	15.0	8.5	4,933	28.2
40	64	17.5	12.4	2,667	32.3
34	71	17.7	10.1	4,480	35.6
46	73	19.3	10.2	4,000	32.4
22	73	20.0	15.5	1,600	30.1
17	75	17.3	17.7	1,787	44.1
15	75	20.7	16.2	1,680	34.4
23	76	16.5	11.9	3,307	36.6
54	107	18.5	14.0	1,360	21.0

[1] Age of the oldest sample tree
[2] Mean maximum height of dominant and codominant trees
[3] Quadratic mean diameter
[4] NA = Not Available

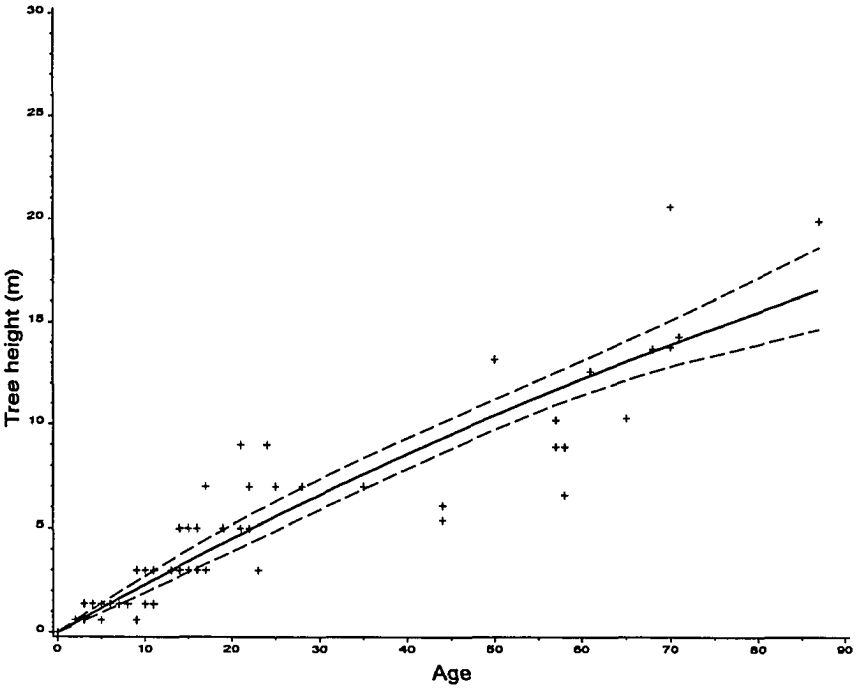
APPENDIX G-1.--ESTIMATED HEIGHT GROWTH FOR OPEN-GROWN *Picea glauca* IN THE **POTR/ARUV C.T.** BROKEN LINES ARE 95 PERCENT CONFIDENCE BANDS FOR MEAN



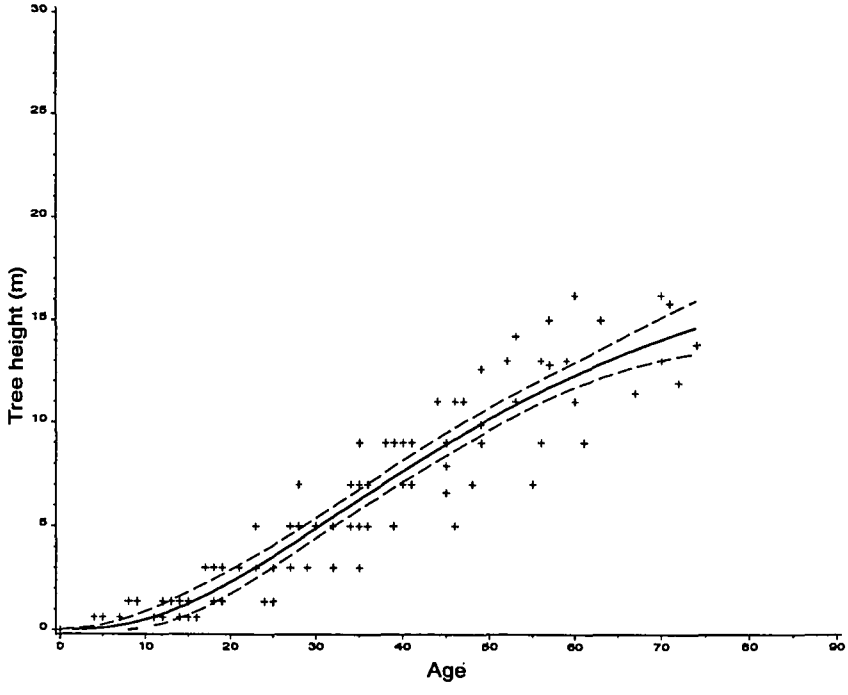
APPENDIX G-2.--ESTIMATED HEIGHT GROWTH FOR SUPPRESSED *Picea glauca* IN THE **POTR/ARUV C.T.** BROKEN LINES ARE 95 PERCENT CONFIDENCE BANDS FOR MEAN



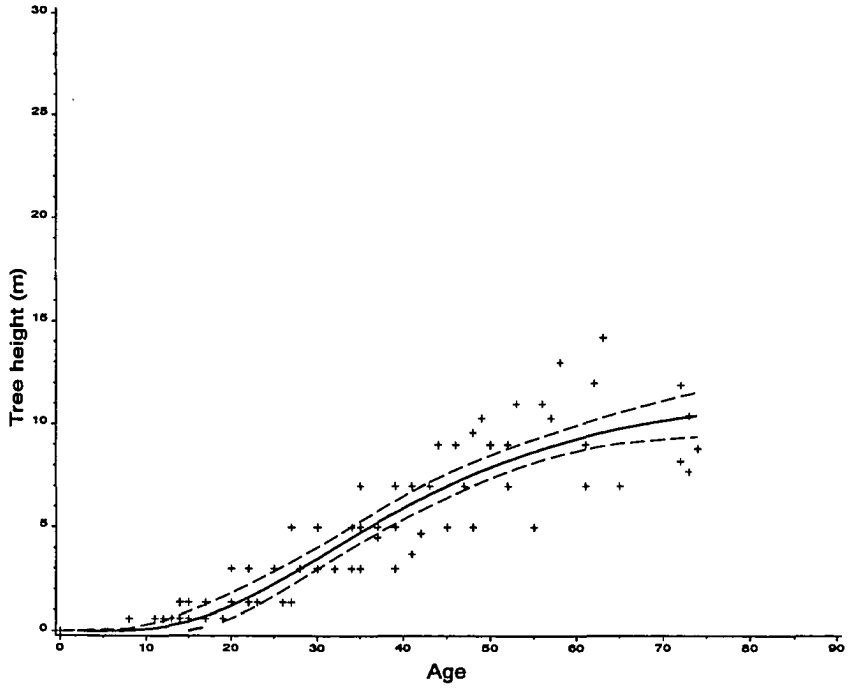
APPENDIX G-3.--ESTIMATED HEIGHT GROWTH FOR *Populus tremuloides* IN THE **POTR/ARUV C.T.** BROKEN LINES ARE 95 PERCENT CONFIDENCE BANDS FOR MEAN



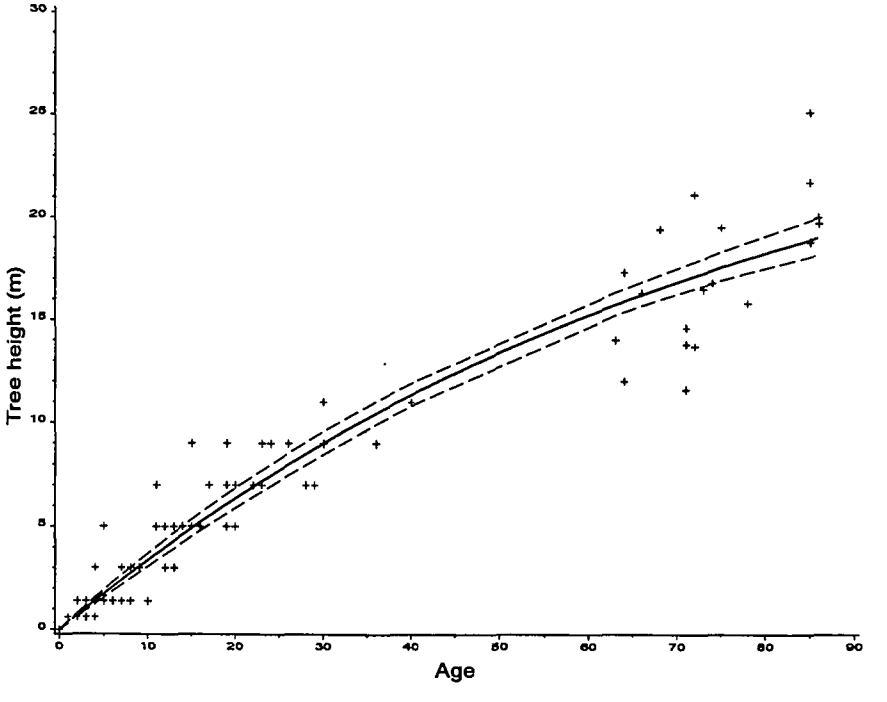
APPENDIX G-4.--ESTIMATED HEIGHT GROWTH FOR OPEN-GROWN *Picea glauca* IN THE **POTR/SHCA C.T.** BROKEN LINES ARE 95 PERCENT CONFIDENCE BANDS FOR MEAN



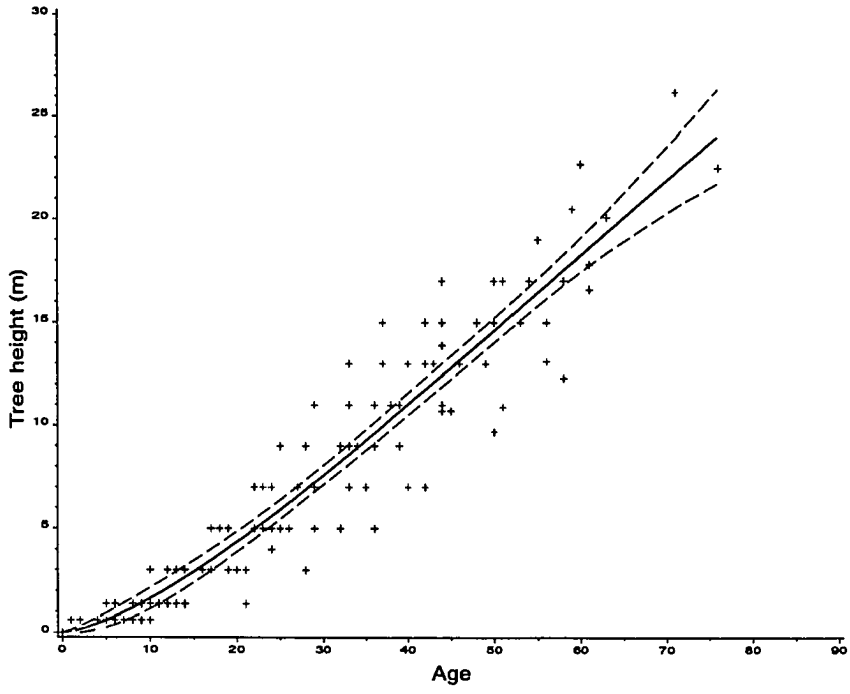
APPENDIX G-5.--ESTIMATED HEIGHT GROWTH FOR SUPPRESSED *Picea glauca* IN THE **POTR/SHCA C.T.** BROKEN LINES ARE 95 PERCENT CONFIDENCE BANDS FOR MEAN



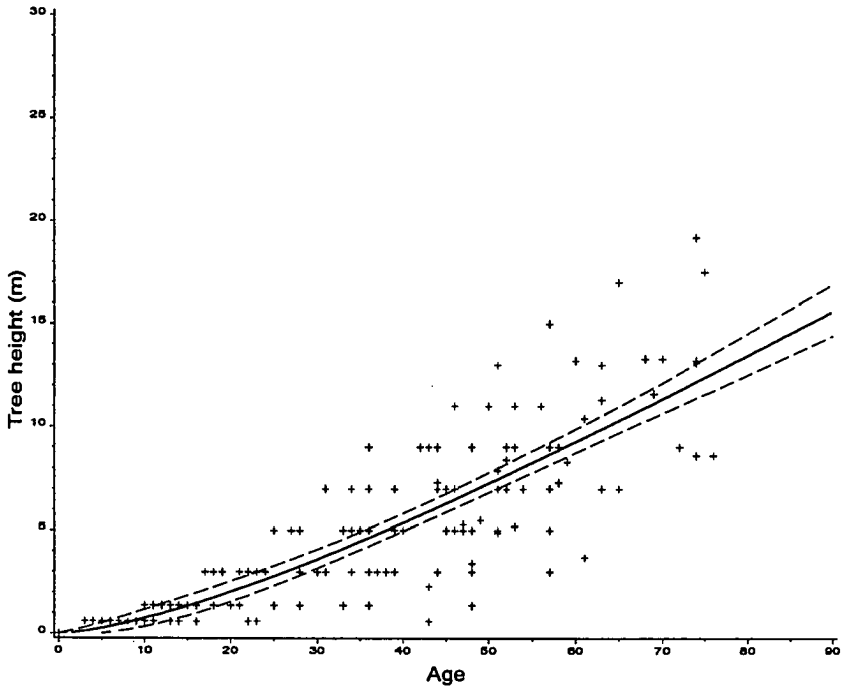
APPENDIX G-6.--ESTIMATED HEIGHT GROWTH FOR *Populus tremuloides* IN THE **POTR/ARUV C.T.** BROKEN LINES ARE 95 PERCENT CONFIDENCE BANDS FOR MEAN



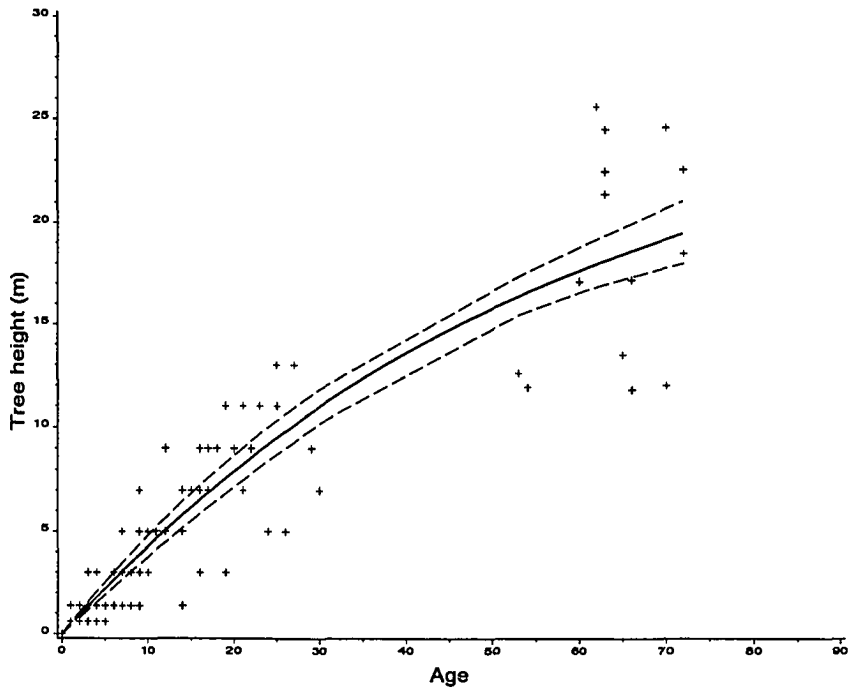
APPENDIX G-7.--ESTIMATED HEIGHT GROWTH FOR OPEN-GROWN *Picea glauca* IN THE **BEPA-POTR/VIED C.T.** BROKEN LINES ARE 95 PERCENT CONFIDENCE BANDS FOR MEAN



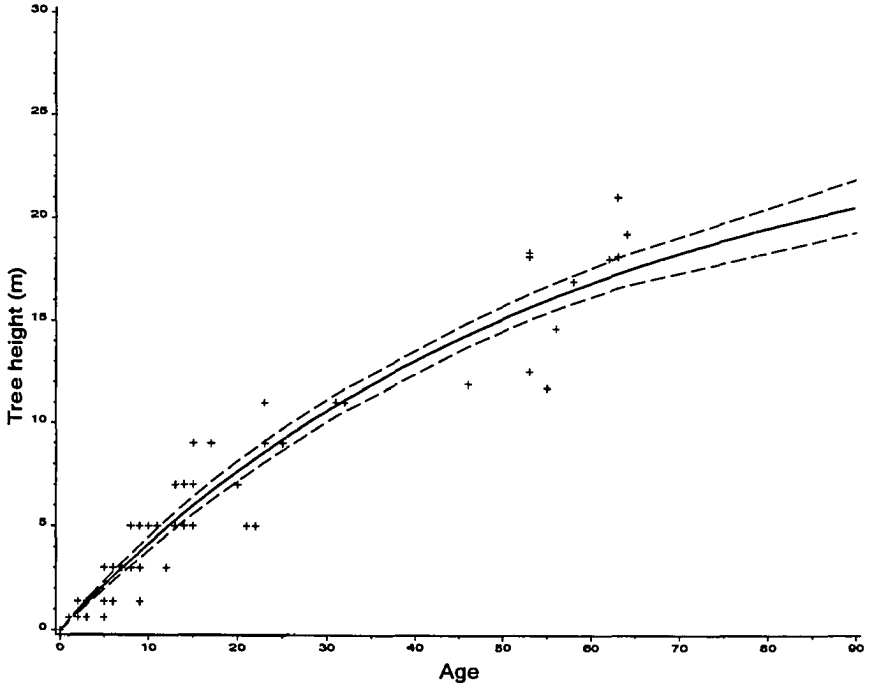
APPENDIX G-8.--ESTIMATED HEIGHT GROWTH FOR SUPPRESSED *Picea glauca* IN THE **BEPA-POTR/VIED C.T.** BROKEN LINES ARE 95 PERCENT CONFIDENCE BANDS FOR MEAN



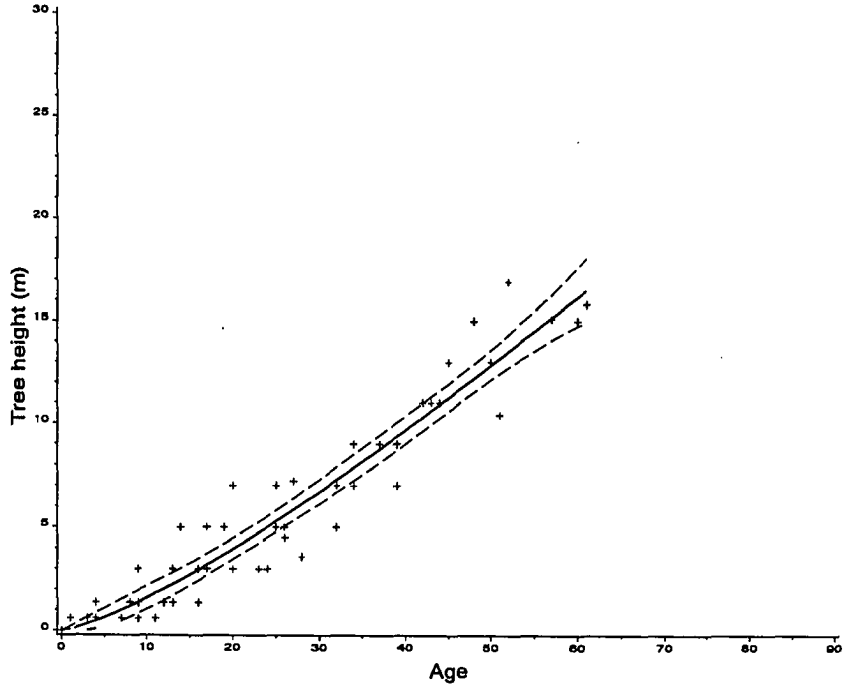
APPENDIX G-9.--ESTIMATED HEIGHT GROWTH FOR *Populus tremuloides* IN THE **BEPA-POTR/VIED C.T.** BROKEN LINES ARE 95 PERCENT CONFIDENCE BANDS FOR MEAN



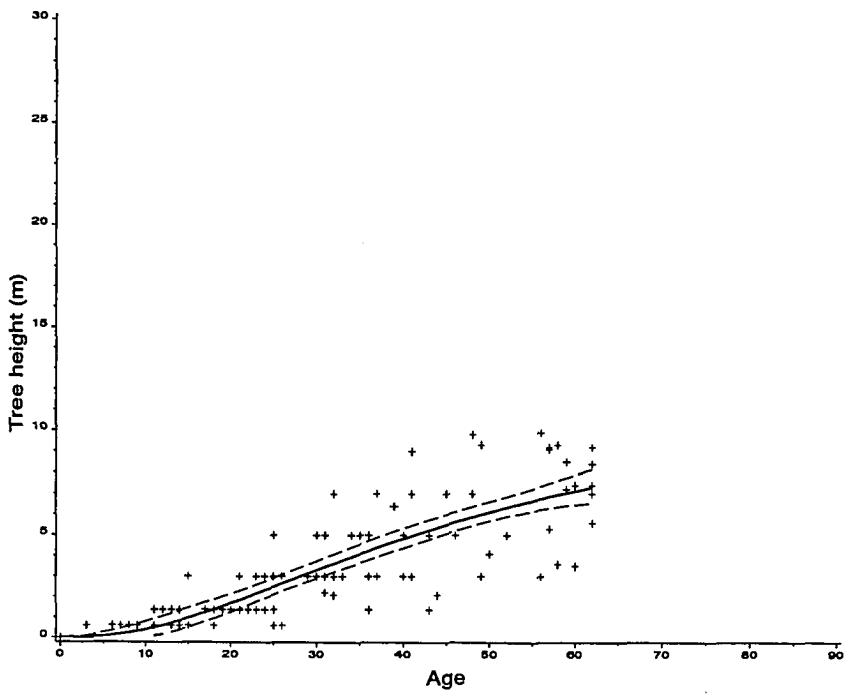
APPENDIX G-10.--ESTIMATED HEIGHT GROWTH FOR *Betula papyrifera* IN THE **BEPA-POTR/VIED C.T.** BROKEN LINES ARE 95 PERCENT CONFIDENCE BANDS FOR MEAN



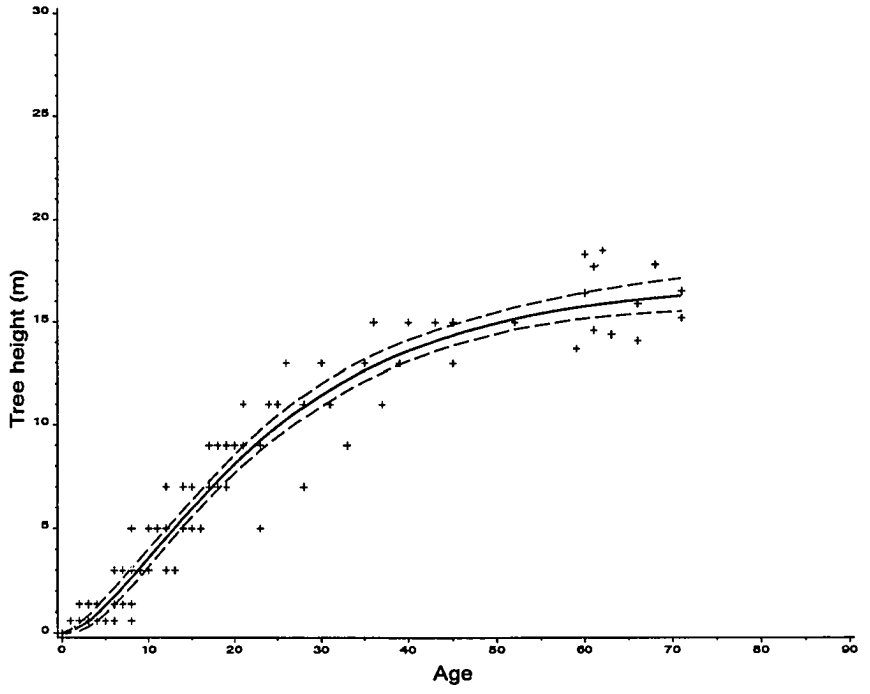
APPENDIX G-11.--ESTIMATED HEIGHT GROWTH FOR OPEN-GROWN *Picea glauca* IN THE **BEPA-POTR/ALCR C.T.** BROKEN LINES ARE 95 PERCENT CONFIDENCE BANDS FOR MEAN



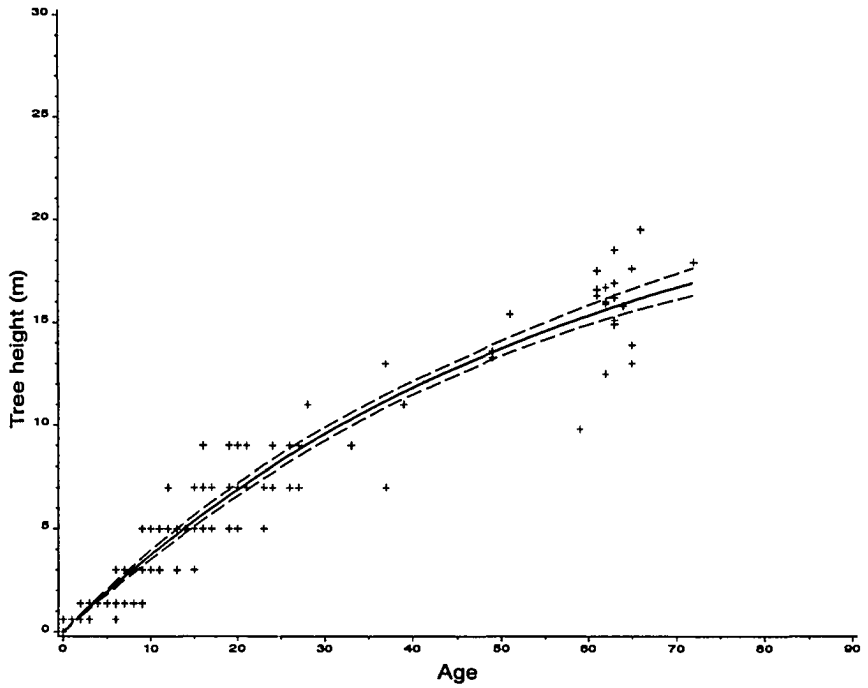
APPENDIX G-12.--ESTIMATED HEIGHT GROWTH FOR SUPPRESSED *Picea glauca* IN THE **BEPA-POTR/ALCR C.T.** BROKEN LINES ARE 95 PERCENT CONFIDENCE BANDS FOR MEAN



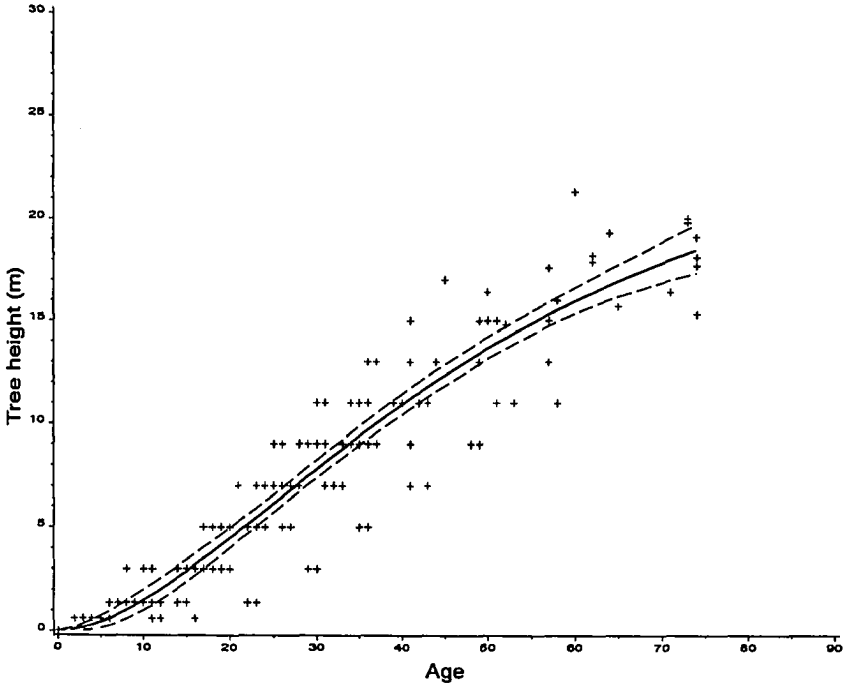
APPENDIX G-13.--ESTIMATED HEIGHT GROWTH FOR *Populus tremuloides* IN THE **BEPA-POTR/ALCR C.T.** BROKEN LINES ARE 95 PERCENT CONFIDENCE BANDS FOR MEAN



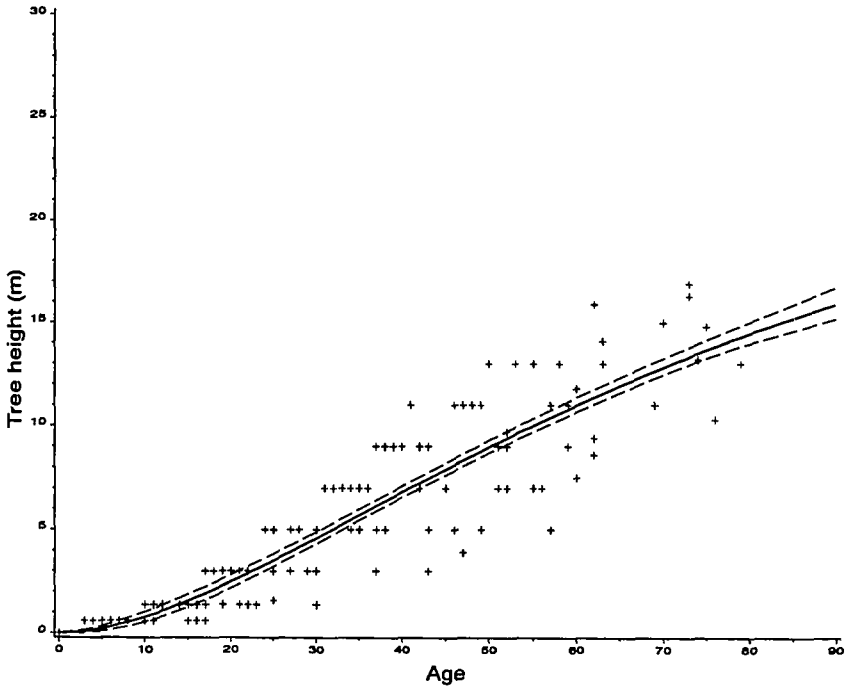
APPENDIX G-14.--ESTIMATED HEIGHT GROWTH FOR *Betula papyrifera* IN THE **BEPA-POTR/ALCR C.T.** BROKEN LINES ARE 95 PERCENT CONFIDENCE BANDS FOR MEAN



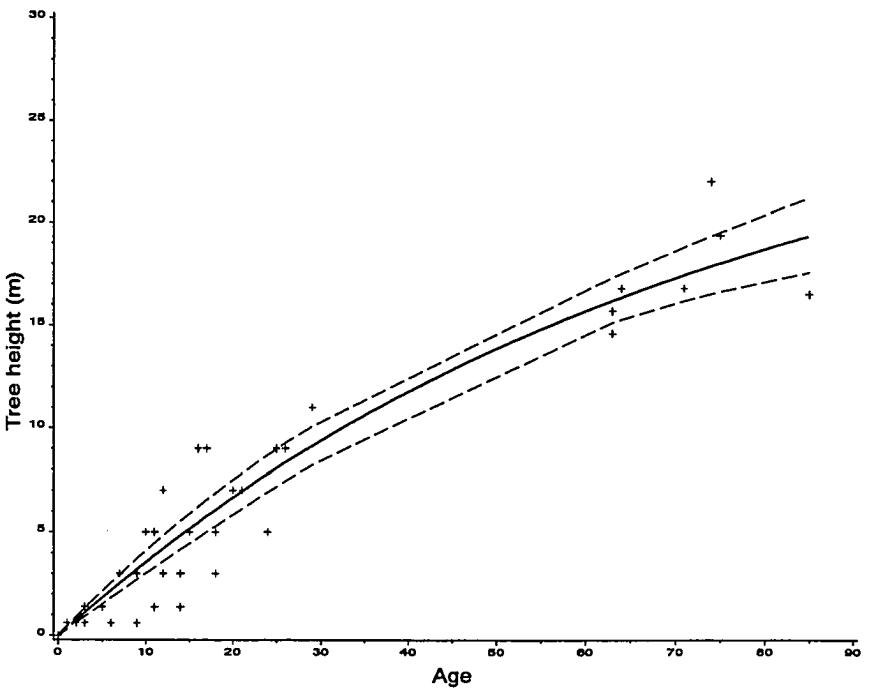
APPENDIX G-15.--ESTIMATED HEIGHT GROWTH FOR OPEN-GROWN *Picea glauca* IN THE **PIGL-BEPA/HYSP C.T.** BROKEN LINES ARE 95 PERCENT CONFIDENCE BANDS FOR MEAN



APPENDIX G-16.--ESTIMATED HEIGHT GROWTH FOR SUPPRESSED *Picea glauca* IN THE **PIGL-BEPA/HYSP C.T.** BROKEN LINES ARE 95 PERCENT CONFIDENCE BANDS FOR MEAN



APPENDIX G-17.--ESTIMATED HEIGHT GROWTH FOR *Populus tremuloides* IN THE **PIGL-BEPA/HYSP C.T.** BROKEN LINES ARE 95 PERCENT CONFIDENCE BANDS FOR MEAN



APPENDIX G-18.--ESTIMATED HEIGHT GROWTH FOR *Betula papyrifera* IN THE **PIGL-BEPA/HYSP C.T.** BROKEN LINES ARE 95 PERCENT CONFIDENCE BANDS FOR MEAN